Institute of Agricultural Sciences in the Tropics
(Hans-Ruthenberg-Institute)

Field: Agroecology in the Tropics and Subtropics

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Estimating Grass Productivity under Different Clipping Frequencies and Rainfall Amount: Implications for Rangeland Responses to Climate Change

A Dissertation

Submitted to the Faculty of Agricultural Sciences in fulfillment of the regulations to acquire the academic degree “Doctor of Agricultural Sciences - doctor scientiarum agriculturae” (Dr. sc. agr. /Ph.D. in Agricultural Sciences)

Presented by

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Stuttgart, 2017

This thesis was accepted as a doctoral Dissertation in fulfillment of the regulations to acquire the doctoral degree “Doktor der Agrarwissenschaften/PhD” by the Faculty of Agricultural Sciences at University of Hohenheim on 14.07.2017.

Date of the oral examination: July 31, 2017

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Author’s Declaration

I, Samuel Tuffa Kawo, hereby declare that I have written this thesis entitled “Estimating Grass Productivity under Different Clipping Frequencies and Rainfall Amount: Implications for Rangeland Responses to Climate Change” independently as my original work as part of my dissertation at the Faculty of Agricultural Sciences at the University of Hohenheim.

All authors in the quoted or mentioned publications in this manuscript have been accredited. No piece of work by any person has been included without the author being cited, nor have I enlisted the assistance of commercial promotion agencies. This thesis has not been presented at any other board for achieving any other academic degree.

Stuttgart, 2017

Samuel Tuffa Kawo

Dedication

I would like to dedicate this piece of work to the memorial of my beloved and unforgettable late son, *Wanufi*, who was a joy to my soul during my field work but left us suddenly.

Acknowledgements

Above all, I would like to thank God for providing me the blessings to complete this work.
I would like to express my deepest appreciation and gratitude to my supervisor, PD. Dr. Anna C. Treydte, for continuous support, teaching, and encouragement. This thesis would not have been achieved without her expertise guidance. She always found time to read the manuscripts and returned faster with insightful comments than one could expect. (Thank you especially for your time, endurance and efforts you have put into my work throughout the study period from afar. You pushed me past my comfort zone, making me feel like everything is within reach and that was how I have acquainted with new methods in my study. I cannot thank you enough for your assistance beyond the academia, especially when I had to pass through the hardest time in my life.) I am also indebted to Professor Emeritus Joachim Sauerborn, the former head of the Agroecology in Tropics and Subtropics department, who officially facilitated my application to join his working group and encouraged me during polishing the research proposal before I left for the field work.

This work could not have been accomplished had I not been supported by local government and non-government offices as well as individuals who have been guiding and sharing their experiences and resources. As such, I extend special thanks to Drs. Abule Ebro and Solomon Desta who recommended me the approach in my experiment during the field work. Further, Drs. Abule Ebro and Getnet Asefa wrote influential letters of recommendations that certainly helped in my admission to "Excellence Scholarship" to participate in FSC's Ph.D. Program, "Global Food Security". A special appreciation is expressed for Dr. Ayana Angassa, for his valuable advice, reassuring and continuous encouragement for Ph.D. study applications. Equal words of thanks go to Feed and Range research team (Bedasa Eba, Asfaw Ejo, Bikila Negasa and Gebeyehu Elias, and Zerihun Yohannes) of Yabello Pastoral and Dryland Agriculture Research Centre (YPDARC) for giving me the seeds of the study species. I am very grateful to all the research staffs that were always around to give a hand when I was in need, esp. during unloading and setting up of the water harvesting tanks as well as during transplanting the seedlings to pots and plots as they had to be transplanted at the same time. Thank you for the very interesting time we had in Yabello, particularly when my family was away as my wife was on a study leave. I apologize the 3F's (the fantastic food fighters) for I could not list your names here; it was great to "watch" the fight sometimes, and that was why I did not like to make your name list public☺. Especial thanks go to my field assistant, Abdella Hamid. I would like also to thank Wako Liban, Jarso Gollo (Borana Zone Water Development and Mines Office), Girma Getachew, Daniel Churqa (Goal Ethiopia-Boran Office) Desta Negewo, Siraj Kelil, Sisay Taye, Dhaba Wirtu, and Bultu Kusa (YPDARC, Natural resource research team), Jatani Huqa and Kanu Boru (Yabello District Rural Road

Construction Office) who lent me water harvesting tanks (for storing the 22,000 liters of water for the experiments) and had waited until I finished my experiments while they themselves had a pressing need for the water tanks. My especial thanks go to Feyisa Saboka, Mohamed Hamid and Fiseha Tadesse, who organized the climate date of the study area, without which calculations to arrive at the watering amount as treatment and the total volume (22,000 liters) of water to be stored for the experiments would not have been possible. I would not have conducted the experiments without their understanding and help. I am very much grateful to Drs. Alexandra Jorge, Abdena Asebe (Forage Gene Bank at International Livestock Research Institute) for providing me the root split of study species for free.

My heartfelt thanks go to my brother, Rev. Dawit, and my father, Tuffa Kawo (Abisho), for their love and consistent encouragement throughout my life. Dave, your generosity, kindness, and spiritual strength have enriched my life in numerous ways. I thank my wife, Addis, who had to go without me for a long time, for her love, care, and support, and for always being there for me and for playing a triple role of wife, mother and student; and to Obsinan, our son (born on Nov. 12, 2014), who endured without complaining our busy academic lives☺.

Numerous people have contributed to this dissertation with fruitful discussions, comments and support along the way. Thanks to all of them, especially to Prof. Dr. Dana Hoag of Colorado State University who organized a meeting and funded my travel to present my research proposal at the East Africa Targeted Investment for Research Impact (EATIRI); I am grateful for also partially funding my field work. Particular thanks to my officemates: Franziska Harich (Franzi) and Reza Golbon, who were very important friends and ready to help. I would like to express my heartfelt gratitude to all staff and colleagues in the department of Agroecology in the Tropics and Subtropics (490f) for all such friendly support and cooperation during my study period, especially Eva Schmidt, Marc Cotter, Inga Häuser, Professor Konrad Martin, Sabine Baumgartner, Regina Belz and Despina Savvidou as well as the ex-staff members (Michael Yongha Bo, Baset Garboni, Lenard Mounde, Hasan Yusuf). Thanks for providing me an intellectually stimulating and lovely working environment. (Entschuldige, Sabine, dass ich dich nicht in die Kaffeepause begleiten konnte; I will let you know if I would start drinking coffee – but, thank you very much for your concern and invitation to take a recess while I was sitting in the office sometimes without respite). Special thanks go to Dr. Frank Rasche, who helped me a lot by facilitating administrative issues in the university when his intervention is needed. I am also thankful to the department secretary, Frau Eva Shmidt, for her assistance in reserving me an accommodation at a lovely German family (Harald, Martina, Lisa, Kai, and Inga) with whom I lived for three years; I am very grateful for their extraordinary assistance. I am deeply thankful to all staff of Food Security Centre (FSC),

especially ex-staff (Dr. Detlef Virchow, Dr. Brigitte Kranz, Helene Stauss, Dr. Andrea Jost) and the present staff (Dr. Jenny Kopsch-Xhema, Dr. Nicole Schönleber and Heinrich Hagel) for all supports and cooperation especially in handling all the administrative matters related to my study and for offering me stimulatory excursions and soft skill trainings and workshops throughout the study period. I have made too many close friends at the university to name, but they know who they are. I owe huge thanks to you all for being good friends. Many thanks go to my Ethiopian friends at the university, especially Getu Bekele, Ashinie Gonfa, Bekele Megersa, Kebede Amenu, and all Ethiopians for being good friends during my stay in the university. Jan Pfister was an amazing extraordinary friend who was always close to Ethiopian students showing/telling how to mix easily with the German culture. (Many thanks, Jan, for being a good friend☺.)

My Ph.D. program would not have been possible without financial support; the support of the Food Security Center (FSC), which is supported by the German Academic Exchange Service (DAAD) with funds of the Germany Federal Ministry for Economic Cooperation and Development (BMZ), is gratefully acknowledged. I duly thank the Dr. Hermann Eiselen PhD Research Grant from the Foundation Fiat Panis to undertake my field research. I also thank PD Dr. Anja Linstädter for accepting to take over the co-reviewing of my PhD dissertation. My heartfelt thanks go to Prof. Dr. Uta Dickhöfer for taking the role of co-reviewer during the colloquium. I am also thankful to Professor Dr. Regina Birner for accepting to be the additional examiner of my thesis defense and Professor Dr. Markus Rodehutscord, representative for Vice dean and head of the committee. Furthermore, I express my deep appreciation to the Oromia Agricultural Research Institute (OARI) for permitting me to pursue my Ph.D. study. I am especially grateful to Dr. Aseffa Taa, Deputy Director General of OARI and my immediate boss, for his encouragement and unreserved support in various ways during my study period. Especial thanks go to Mr. Eshetu Teshome, the then director of YPDARC for allowing me to use the center's facility, particularly the laboratory as I had to dry the clipped samples immediately after clipping. Mr. Abiyot Lelisa, head of the laboratory, deserves special thanks for his help in the sample preparation and analysis and for taking care of my samples while I was away for other reasons.

I am quite sure that there are lots of people who contributed to my achievement in one way or another, but whom I failed to list their names. I apologize for missing your names in the acknowledgments.

Samuel Tuffa Kawo

Summary

Resilience and sustainable use of rangelands depend on pre- and post-degradation management. A sustainable rangeland use can be achieved by maintaining its productivity in the long run. Herbivory and drought are the two main stressors reducing the primary production of rangelands and, hence, related ecosystem functions and services as well as livestock production. In semiarid rangelands, herbivore populations can be kept at its varying carrying capacity through encouraging animal harvesting when forage production decreases to avoid rangeland degradation. Degraded areas can also be restored through reseeding with appropriate local species to enhance rangeland resilience, particularly given the current and projected impacts of climate change to cope with the rapid disappearance of species and ecosystem services. However, it is unclear how grass species currently used in the reseeding respond to combined effects of herbivory and drought and how grazing cattle populations change under the current and the predicted increasing drought frequency.

The Borana rangeland, Ethiopia, had been highly productive and an important forage resource for livestock. However, its productivity has been reducing as a result of degradation, mainly caused by recurrent drought, land use change, livestock overgrazing and bush encroachment. Reseeding as a management strategy for the restoration of degraded rangelands and their ecosystem services has been urgently recommended. This is particularly urgent as in the face of human population increase a high demand for meat as a protein source is expected and mitigation strategies to capture CO_2 from the atmosphere in the face of climate change is needed. Rangeland restoration through reseeding of palatable grass species can improve both structural and functional vegetation characteristics, which will also enhance food security. The main rangeland ecosystem services include, amongst others, provision of animal feeds (biomass and nutrients) and carbon (C) storage to capture CO_2 from the atmosphere. However, the post reseeding rangeland management is still lacking knowledge on grass biomass allocation, nutrient and C storage under the influence of herbivory and drought. In addition, the belowground biomass and C storage of grasses have been rarely studied in grasslands, and in this study, we quantified these two variables under the two major grass stressors, clipping and irrigation (simulated herbivory and rainfall regime, respectively). This dissertation aimed at filling this knowledge gap of pre- and post-reseeding rangeland management in order to inform policy makers for devising an appropriate strategy for a sustainable use of rangeland resources. Responses of two dominant perennial grass species (*Cenchrus ciliaris* and *Chloris gayana*) frequently used in reseeding to simulated herbivory and rainfall regimes were assessed in pot and field plot experiments on young grasses. Further, we addressed how herbivory influences biomass allocation, nutritive values and C storage in mature tufts of these two native grasses under ambient rainfall conditions.

The responses of biomass and C storage showed contrasting results across grass age as well as species. Generally, the clipping/grazing strongly triggered the belowground biomass allocation and enhanced C storage of *C. ciliaris* tufts while *C. gayana* tufts differed only slightly. In both mature grasses, however, clipping highly reduced aboveground biomass and C storage. In contrast, for the young grass seedlings, moderate and light clipping triggered regrowth and, hence, biomass and C storage in both above- and belowground parts. Meanwhile, reduced irrigation showed the same effect on biomass allocation and C storage in both study grasses. Lower irrigation highly reduced biomass and C in both above- and belowground parts.

The results presented in this dissertation highlight that the effects of herbivory and rainfall variability, as well as grass maturity, should be incorporated into the management of rangelands. Our experiments established the first interactive effect of herbivory and rainfall on the biomass allocation and C storage of mature and young grasses in the semiarid Borana rangelands, Ethiopia. Knowledge of these interacting factors is deemed essential for policy makers to develop a sound rangeland management policy that can enhance the C storage potential of degraded rangelands under climate change and, hence, the mitigation and adaptation strategies through improved post restoration of degraded areas.

We also modeled cattle population dynamics under a varying carrying capacity and stochastic environmental conditions, which has never been done before in the semi-arid Borana rangeland ecosystem. Modeling cattle population dynamics is essential for capturing changes in population responses to climate change in a variable social and ecological environment at a large temporal scale. We developed and evaluated a novel Boran cattle population trajectory model under different drought frequency events, using differences in vital rates among age- and sex-classes as well as a varying carrying capacity. Stochasticity was built into the model by allowing droughts to occur randomly within model runs in Berkeley Madonna software, with different long-term average drought frequencies characterizing the individual four model scenarios. The model result indicated that reduction in rainfall, i.e., increasing drought frequency - as predicted for Borana - leads to a high loss in cattle populations. The overall population size was highly sensitive to the sale of juvenile as well as mature female cattle when drought hit the system. The stochastic population modeling under varying carrying capacity in the face of increasing drought scenarios indicated the livelihood challenges ahead for the pastoral community. Cattle populations must be limited timely and grass productivity must be enhanced in a sustainable way in the face of climate change. Therefore, this dissertation aimed at rangeland pre- and post-degradation management suggestions by modeling cattle populations and through grass experiments, respectively.

Management should focus on lowering cattle herd crashes through increasing sale of mature males that increases feed availability to females during drought years in the Borana Rangelands as well

as enhancing the resilience capacity of rangelands through maintaining healthy conditions and restoring degraded areas. Further, drought early-warning systems and market information must be strengthened so that pre-planned selling can be realized for the fair and sustainable use of the animal resource. Pastoralists would benefit from this approach as they could sell their animals before drought wipes out their cattle in huge numbers.

German Summary /Zusammenfassung/

Die Widerstandsfähigkeit und Nachhaltigkeit von Weideland hängt von dem Management vor und nach Degradierungen ab. Eine nachhaltige Nutzung von Weideland impliziert den langfristigen Erhalt der Produktivität. Beweidung und Dürren sind zwei der Haupt-Stressfaktoren, welche die Primärproduktion von Weideland reduzieren und damit sowohl zugehörige Ökosystemfunktionen und –dienstleistungen als auch die Tierproduktion beeinträchtigen. Semiaride Weideländer mit variierender Tragfähigkeit können zur Weidetierhaltung genutzt werden, indem die Herdengröße bei nachlassender Futterproduktion verringert wird. Eine Schädigung des Weidelandes kann so vermieden werden. Bereits degradierte Flächen können durch das Wiederaussäen geeigneter lokaler Arten wiederhergestellt werden um die Widerstandsfähigkeit des Weidelandes zu verbessern. Angesichts der Folgen des derzeitigen und vorhergesagten Klimawandels ist dies von besonderer Bedeutung um dem rasanten Verschwinden von Arten und Ökosystemdienstleistungen entgegen zu wirken. Dennoch ist unklar wie die derzeit zur Aussaat verwendeten Grasarten auf die kombinierten Effekte von Beweidung und Dürre reagieren und wie sich grasende Rinderherden unter der derzeitigen Dürre und den vorhergesagten zunehmenden Trockenheitsperioden verändern werden.

Das Borana Weideland in Äthiopien war einst eine hoch produktive und bedeutende Futterquelle für Weidevieh. In Folge wiederkehrender Dürren, Landnutzungswandel, Überweidung und Verbuschung hat diese Produktivität jedoch stetig abgenommen. Das Wiederaussäen geeigneter lokaler Arten wurde als Managementmaßnahme dringend empfohlen, um das degradierte Weideland und dessen Ökosystemdienstleistungen wieder aufzuwerten. Dies ist von besonderer Wichtigkeit, da angesichts des Bevölkerungswachstums eine zunehmende Nachfrage nach Fleisch als Proteinquelle erwartet wird und im Hinblick auf den Klimawandel schadensmindernde Maßnahmen ergriffen werden müssen um CO_2 aus der Atmosphäre zu filtern. Weidelandrestaurierung durch Aussähen von schmackhaften Grasarten kann sowohl die strukturellen als auch die funktionalen Vegetationseigenschaften verbessern, was zudem zu einer Förderung der Ernährungssicherheit beiträgt. Zu den wichtigsten Ökosystemdienstleistungen von Weideland gehören unter anderem die Bereitstellung von Tierfutter (Biomasse und Nährstoffe) und die Kohlenstoffspeicherung (C) um CO_2 aus der Atmosphäre zu filtern. Allerdings mangelt es an Wissen über die Verteilung der Biomasse in den Gräsern, sowie deren Nährstoff- und Kohlenstoffspeicherung unter dem Einfluss von Beweidung und Dürre nach der Aussaat. Hinzu kommt, dass die unterirdische Biomasse- und Kohlenstoffspeicherung von Gräsern bisher kaum untersucht wurde. In dieser Studie quantifizierten wir diese zwei Variablen unter den zwei Haupt-Stressfaktoren für Gräser, Schnitt und Bewässerung (entsprechend eines simulierten Beweidungs-

und Niederschlagsregimes). Ziel dieser Dissertation war es, die Wissenslücken im Vor- und Nachbehandlungsmanagement von Aussaaten auf Weideflächen zu schließen und Entscheidungsträger darüber zu informieren wie angemessene Strategien für eine nachhaltige Nutzung von Weideland entwickelt werden können. Die Reaktionen auf simulierte Beweidungs- und Niederschlagsintensitäten von zwei dominanten mehrjährigen Grasarten (*Cenchrus ciliaris* und *Chloris gayana*), welche oftmals bei den Aussaaten verwendet werden, wurden an jungen Gräsern in Topf- und Feldversuchen untersucht. Zudem analysierten wir, wie sich die Beweidung unter natürlichen Niederschlagsbedingungen auf die Verteilung von Biomasse, Nährwerten und Kohlenstoffspeicherungen in ausgewachsenen Grasbüscheln dieser zwei einheimischen Grasarten auswirkt. Die Ergebnisse zeigten gegensätzliche Reaktionen der Biomasse- und Kohlenstoffspeicherung, abhängig von Alterskategorie und Grasart. Generell löste der Schnitt bzw. die Beweidung eine starke Umverteilung auf die unterirdische Biomasse aus und förderte die Kohlenstoffspeicherung von *C. ciliaris* Büscheln, während *C. gayana* Büschel nur geringfügige Abweichungen zeigte. Bei beiden ausgewachsenen Gräsern reduzierte der Schnitt jedoch die überirdische Biomasse und Kohlenstoffspeicherung stark. Im Gegensatz dazu förderte ein moderater und leichter Schnitt bei jungen Gräsern erneutes Wachstum und damit auch die Biomasse- und Kohlenstoffspeicherung sowohl in über- als auch unterirdischen Pflanzenteilen. Derweil zeigte eine reduzierte Bewässerung den gleichen Effekt auf die Biomasseverteilung und Kohlenstoffspeicherung in beiden untersuchten Grasarten. Geringere Bewässerung reduzierte die Biomasse und den Kohlenstoff in unter- und oberirdischen Pflanzenteilen stark.

Die in dieser Dissertation präsentierten Ergebnisse unterstreichen, dass sowohl die Effekte von Beweidung und variablem Niederschlag als auch das Grasalter im Management von Weideflächen berücksichtigt werden sollte. Unsere Experimente sind der erste Nachweis der interaktiven Effekte von Beweidung und Niederschlag auf die Verteilung von Biomasse und auf die Kohlenstoffspeicherung in alten und jungen Gräsern der semiariden Borana Weideflächen in Äthiopien. Das Wissen um diese interagierenden Faktoren gilt als essentiell für Entscheidungsträger, um ausgewogene Managementstrategien für Weideländer zu entwickeln. So kann das Potenzial zur Kohlenstoffspeicherung in degradierten Weideflächen in Zeiten des Klimawandels verbessert und damit auch schadensmindernde Maßnahmen und Anpassungsstrategien durch verbessertes Nachbehandlungsmanagement von degradierten Flächen unterstützt werden.

Weiterhin modellierten wir die Dynamik von Rinderpopulationen unter variierenden Tragfähigkeits-Kapazitäten und unter stochastischen Umweltbedingungen. Das Modellieren von Dynamiken der Rinderpopulationen wurde noch nie zuvor für das semiaride Borana Weideland

durchgeführt, ist jedoch essenziell um Änderungen von Populationsreaktionen auf den Klimawandel in einer variablen sozialen und ökologischen Umwelt über ein größeres Zeitfenster hinweg registrieren zu können. Wir entwickelten und evaluierten ein neuartiges Boran Rinderpopulationen-Kurvenmodell unter verschiedenen Dürrefrequenz-Vorkommnissen, für welches wir sowohl unterschiedliche Geburten- und Sterberaten innerhalb der Alters- und Geschlechtsklassen als auch variierende Tragfähigkeits-Kapazitäten verwendeten. Die Stochastik wurde berücksichtigt, indem Dürreereignisse zufällig in das Modell eingebunden wurden. Verwendet wurde dafür die Berkeley Madonna Software. Dabei charakterisierten verschiedene langfristige durchschnittliche Dürrefrequenzen die vier individuellen Modellszenarien. Das Ergebnis des Modells deutet darauf hin, dass eine Reduzierung des Niederschlags, zum Beispiel bei zunehmender Dürrefrequenz wie für Borana vorhergesagt, zu einem großen Verlust innerhalb der Rinderpopulationen führt. Die gesamte Populationsgröße reagierte hochsensibel auf den Verkauf sowohl von Jungtieren als auch von erwachsenen weiblichen Rindern, wenn ein Dürreereignis im System stattfand. Das stochastische Populationsmodell mit verschiedenen Tragfähigkeits-Kapazitäten weist angesichts zunehmender Dürreszenarien auf die zukünftigen Herausforderungen für die Lebensgrundlage der auf die Weidewirtschaft angewiesenen Gemeinschaften hin. Rinderherden müssen rechtzeitig verkleinert werden und die Grasproduktivität angesichts des Klimawandels auf nachhaltige Weise gefördert werden. Aus diesem Grund konzentrierte sich diese Dissertation auf Vorschläge zum Vor- und Nachbehandlungsmanagement von degradierten Weideflächen durch Modellierung von Rinderpopulationen und der Durchführung von Grasexperimenten.

Das Management sollte sich darauf konzentrieren, dem Kollaps von Rinderherden vorzubeugen, indem der Verkauf von ausgewachsenen Stieren gesteigert wird. Dadurch werden Futterressourcen für die weiblichen Tiere während Dürrejahren in den Borana Weideländern frei. Gleichzeitig muss die Widerstandsfähigkeit der Weideflächen verbessert werden, indem gesunde Bedingungen beibehalten und degradierte Gebiete restauriert werden. Weiterhin müssen Frühwarnsysteme für Dürren und Marktinformationen gefördert werden, damit im Voraus geplante Verkäufe der Tierressourcen auf faire und nachhaltige Weise realisiert werden können. Dieser Ansatz würde zudem den Viehhaltern Vorteile durch den Verkauf der Tiere bringen, da ein großer Verlust von Rindern in Folge von Dürren vermieden werden könnte.

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List of acronyms and abbreviations

AG_B	Aboveground grass biomass
agC	Aboveground grass carbon
ANOVA	Analysis of variance
BG_B	Belowground grass biomass
bgC	Belowground grass carbon
C	Carbon
CDKN	Climate and Development Knowledge Network
cm	centimeter
CO_2	Carbon dioxide
CSA	Central Statistical Agency
FAO	Food and Agriculture Organization (United Nations)
GLM	General Linear Model
HLPE	The High Level Panel of Experts
IIED	International Institute for Environment and Development
ILCA	International Livestock Center for Africa
ILRAD	International Laboratory for Research on Animal Diseases
ILRI	International Livestock Research Institute
IPCC	Intergovernmental Panel on Climate Change
LSD	Fisher's least significant difference
masl	Meters above sea level
mio	million
mm	millimeter
Pers. Comm.	Personal Communication
R^2	coefficient of determination
REGLAP	Regional learning and advocacy program for vulnerable dryland communities
SAS	Statistical Analysis System
SD	standard deviation
SE	standard error
TLU	Tropical livestock unit
WRI	World Resources Institute
YPDARC	Yabello Pastoral and Dryland Agriculture Research Centre

Chapter 1: General introduction

1.1: An overview of rangelands

Rangelands are dominated by herbaceous plants that are grazed by domestic and wild animals (WRI/IIED, 1986). Areas that are not developed, not cultivated, not forested and not solid rock or ice and that include grasslands, savannahs, steppes, shrublands, deserts and tundra can be classified as rangelands; they are found on every continent (Fynn et al., 2010; Soussana et al., 2010). Most of the rangelands are found in marginal areas, i.e., the drylands of the world, which cover about 45% of terrestrial ecosystems (Schimel 2010; Fig. 1.1). The mode of rangeland utilization is mainly extensive animal grazing and the natural resources of rangeland vegetation provides about 70% of the feed for domestic ruminants (Lund, 2007). Further, rangelands are one of the major terrestrial ecosystems that serve as an important carbon sink (Cook et al., 2013). However, nowadays rangelands are under stress due to overgrazing, which is further aggravated by effects of climate change (Acharya et al., 2012). Above average precipitation, varying in its extremes, and frequent drought events will characterize the climate of the future (Trenberth et al., 2014). Drought is expected to become more frequent in dry ecosystems and will negatively affect rangeland productivity and, hence, their goods, functions and services (Desta, 2006).

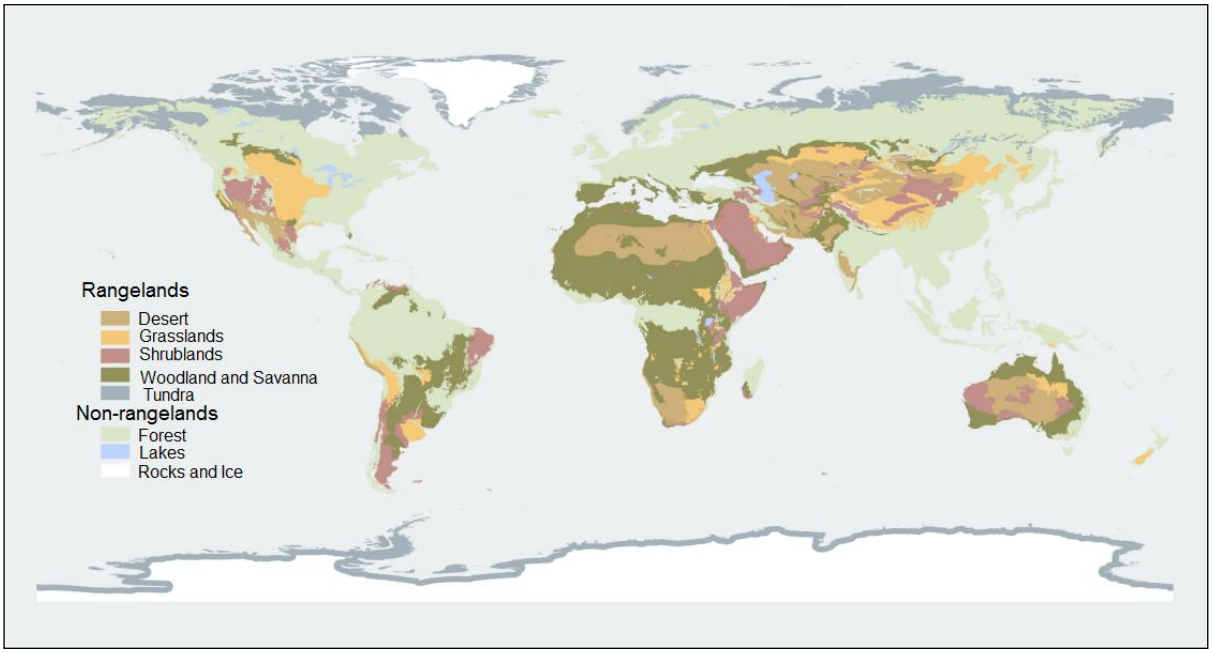

Figure 1.1 Rangelands of the world classified into five different land-cover classes.

Source:

http://www.webpages.uidaho.edu/what-is-range/rangelands_map.htm

1.2: Present challenges to African rangelands

The rangelands in Africa are located in drylands characterized by highly variable climatic elements; their production system is mobile pastoralism, a strategy that has been developed over centuries to cope with the prevalent highly variable climate and, thus, resources (Niamir-Fuller, 1999). In Eastern African drylands, specifically arid and semi-arid lands cover vast areas, which account for more than 63% of the land cover of, e.g., Ethiopia, (Regional Learning and Advocacy Programme (REGLAP) 2012).

Most grazing lands in arid and semiarid regions are highly fragile as they are located in marginal lands that have low productivity due to low soil moisture and low and erratic rainfall (Parton et al., 1994). Global climate change will likely enhance the problem of low rangeland productivity (Fay et al., 2000). Changes in rainfall regime, rather than temperature or CO_2, constitute the most important component of climate change in semiarid areas, where water is the primary limiting resource (Miranda et al. 2011; Shafran-Nathan et al. 2012). The lifestyle of people in the pastoral environment is dictated by two major concepts. In the dryland ecosystem, the driving factor of primary production is climate (and management is dictated by the non-equilibrium concept) while in humid ecosystems, herbivory and anthropogenic activities drive primary production (and management is dictated by the equilibrium concept) (Fig. 1. 2). We combined the two concepts, and readers may refer to other papers (Desta and Coppock, 2002; Sasaki, 2010; Vetter, 2005) to understand how the two concepts integrate in a semiarid ecosystem. In such an ecosystem, devising effective grazing management strategies is difficult owing to the low and highly variable rainfall amounts (Abdul-Aziz, 2010).

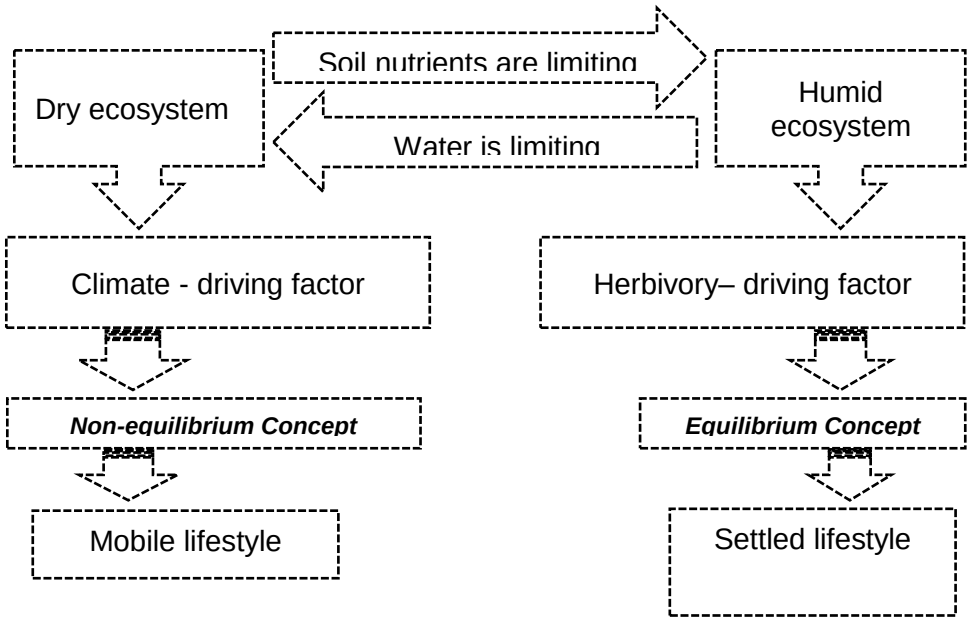

Figure 1.2 Schematic representation of characteristics of the pastoral environment. Derived from Niamir-Fuller 1998.

Global climate change is predicted to alter the growing season rainfall patterns, potentially reducing total amounts of growing season precipitation and redistributing rainfall into fewer but larger individual events (Fay et al., 2000). Such rainfall shifts may have considerable impact on grass productivity. Climate change will result in multiple stresses for animals and plants, and yet, it is unknown how these stresses may combine in rangeland systems over the coming decades (HLPE, 2012). The productivity of rangeland ecosystems is predominantly affected by drought and herbivory (Baruch and Jackson, 2005). However, currently there is little information available on the impacts of climate change on the productivity of rangeland grasses per se. Grasslands sequester and store a large amount of soil carbon, and this storage is primarily controlled by herbivory and precipitation (Chimner and Welker, 2011). Increasing global demand for livestock products (FAO, 2003) in combination with declining land area available for livestock grazing due to changes in land use (Haile et al., 2010) has enhanced the pressure onto rangelands over the last decades. Moreover, woody plant encroachment, lack and/or shortage of rain and ban of rangeland burning were among the major factors that caused rangeland deterioration, particularly in the Borana rangelands, southern Ethiopia (Gemedo-Dalle et al., 2006). Up to now, only few studies have investigated how the combined effect of climate change and grazing pressure affects in particular the herbaceous vegetation (Fynn and O'Connor, 2000; Pandey and Singh, 1992).

1.2.1: Rangeland management options

Rangeland degradation directly affects livestock production, which the livelihood of pastoralists depends upon, resulting in food insecurity and ecological instability (Dalle et al., 2009). In Borana, a shift in vegetation from grass to woody plants has severely affected cattle production over the last decades (Dalle et al., 2006). Thus, alternate livestock species such as camels or goats, who can browse on bushes and trees, might be better adapted to these bush-encroached rangelands under pressure (Angassa, 2002; Solomon et al., 2007). As cattle have been referred to as the true "economic engine" of the system, emphasizing on a sustainable productivity of cattle is a crucial aspect (Coppock et al., 2014). The community-based conservation efforts of the typical Ethiopian Boran cattle (*Bos indicus*) will require securing adequate grazing and water resources (Homann et al., 2003). However, those grass species that are perceived by the pastoralists as highly palatable and desirable, are currently decreasing in both quality and quantity in the Borana rangelands, southern Ethiopia (Angassa, 2002; Solomon et al., 2007). A reason for this decline has been claimed to be disturbances from overgrazing and climate change (Abule et al., 2007; Angassa, 2005; Angassa and Oba, 2010; Haile et al., 2010). While appropriate management of livestock density in rangelands is essential for sustainable production and grassland ecosystem health (Sternberg et al., 2000) the management of dryland ecosystems is mired in controversy due to the

complexity of the ecosystem, despite clear differences between the two management concepts (Fig. 1.2). This region is categorized as non-equilibrium environment, though at times it experiences equilibrium (Desta and Coppock, 2002), which makes the management of the Borana rangelands highly complex. A better understanding of grass productivity and its controlling factors in modern savanna ecosystems could be a key to understanding the productivity of savannas and to predict responses to future climatic changes. Development of effective management strategies for responding to climatic variability is often impeded by the lack of a system framework for analyzing livestock stocking policies and management practices (Bank World, 2005; Kamara et al., 2004). Further, effective decision making requires an understanding of the important biotic and abiotic components of rangeland systems (Fig. 1.3), such as the response of rangeland vegetation to herbivory and climatic change as well as cattle population dynamics. Previous vegetation studies of the Borana rangelands focused mainly on taxonomic descriptions and rangeland condition assessments and reseeding (Angassa and Baars, 2000; Dalle et al., 2009; Haile et al., 2010; Oba and Kotile, 2001; Tebeje et al., 2014). Reseeding of degraded rangelands is a potential management option in eastern African rangelands to enhance the resilience of rangelands. Therefore, it is high time to understand how the native perennial grass individuals respond to increased herbivory under higher drought frequency after reseeding. To bridge this knowledge gap, we conducted clipping (simulated grazing) and irrigation (simulated rainfall variability) experiments on two native grass species, which are commonly used for reseeding, i.e., *Chloris gayana* Kunth and *Cenchrus ciliaris* L., in the Borana rangelands. We further modeled cattle dynamics, combining the equilibrium and non-equilibrium concepts to understand possible future population trajectories under varying environmental scenarios (Fig. 1.3).

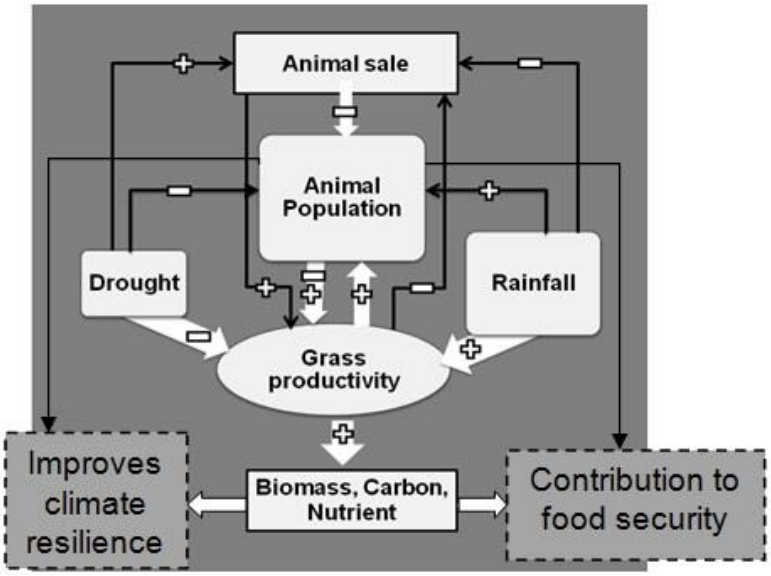

Figure 1.3 Schematic representation of interactions among a rangeland's biotic and abiotic components, the principle we used in cattle population modeling. The plus and/or minus signs stand for positive and negative feedbacks, respectively.

1.2.2: Study plant species

In Borana, particularly two grass species (*C. ciliaris* and *C. gayana*) are important for cattle productivity as they are highly palatable, native to the study area. These two species further have a vast global coverage (Fig. 1.4), highlighting their importance for rangeland management. Both grass species have been recommended (Koech et al., 2015; Tebeje et al., 2014) and used for reseeding degraded grazing lands to increase forage production and carbon (C) stocks (Conant et al., 2001; Marshall et al., 2012). *Cenchrus ciliaris* is regarded as one of the native herbaceous forage species that are nutritious all year round and at all growth stages and, thus, is recommended for reseeding (Coppock, 1994). Likewise, *C. gayana* is also an important native perennial grass species that has been used for rehabilitation of degraded Borana rangeland (Tebeje et al., 2014). However, there is a lack of information as to the management options of the reseeded grass in the face of climate change as well as their resilience against grazing, their shifts in nutrient and carbon content under varying rainfall and grazing pressure.

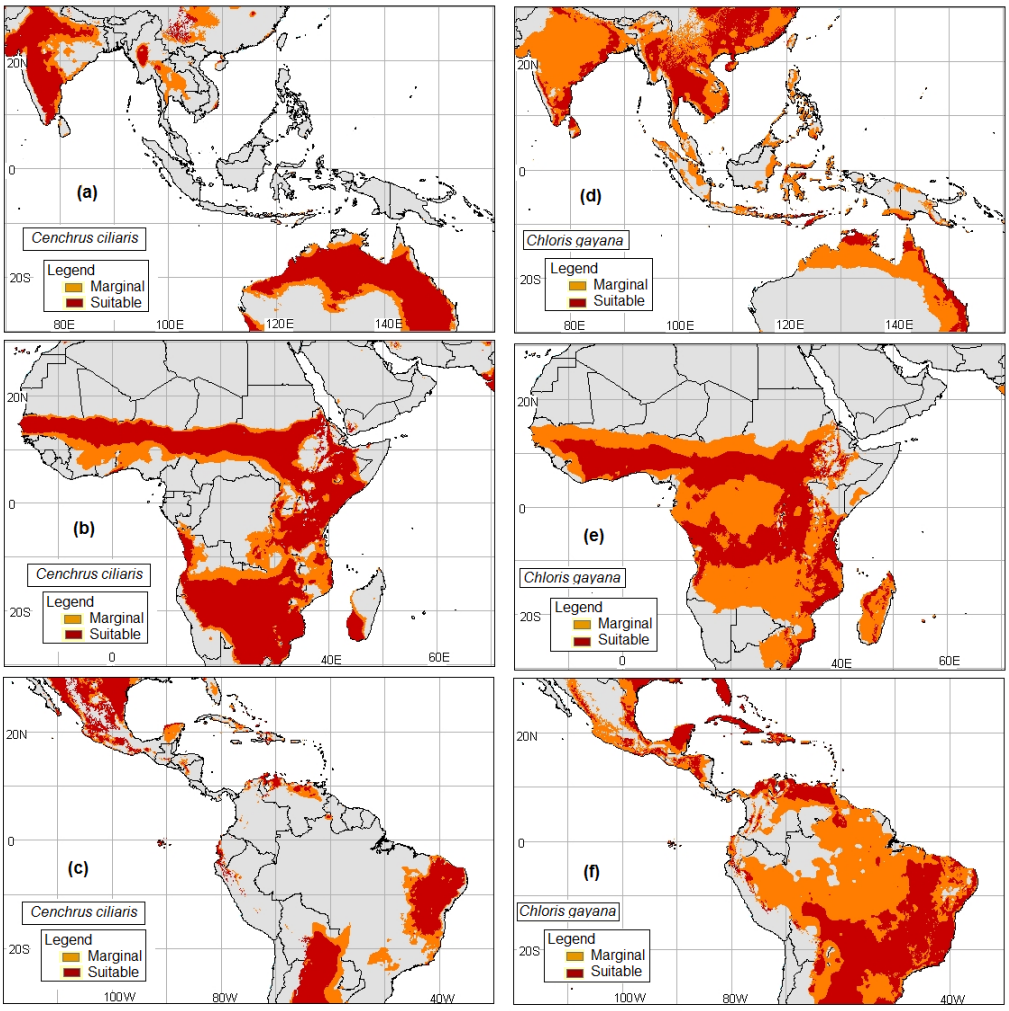

Figure 1.4 Global distribution and native habitat (marginal and suitable) of *C. ciliaris* (a-c) and *C. gayana* (d-f) grass species across the varying continents in 2005.

(Modified from http://www.tropicalforages.info/key/Forages/Media/Html/).

Studies regarding the influence of water limitation in grasslands of other parts of the world indicated that water strongly limits annual productivity (Knapp et al. 2001; Knapp et al. 2008; Fig. 1.2). While experiments on altering rainfall regime have been widely conducted across many countries (Knapp et al., 2008, 2006), most of these studies have been carried out in mesic grasslands and experiments are missing in East African dry rangelands (Fidelis et al., 2013). These types of studies, however, are critical for assessing the impact of climate change on the provisioning of key ecosystem services (Weltzin et al., 2003) and increase the accuracy of predictions of ecosystem responses to global climate change (Snyman, 2009). Grasslands are important and tractable systems for examining these issues because they cover a large proportion of terrestrial land mass, are rich and dynamic in biodiversity, are a globally important agricultural resource, and are at risk from degradation and habitat conversion (Fay et al., 2011). Thus, understanding how rainfall variability and grazing affects grass productivity is critical to forecast changes in rangeland productivity and carbon storage potential under future climate scenarios. Further, appropriate management of livestock populations in arid and semiarid rangelands through local pastoralists in the face of climate change will strongly depend on this knowledge.

1.2.3: Cattle population size in the face of climate change

Eastern Africa has the largest ruminant population in Africa (ILCA/ILRAD, 1988). Ethiopia harbors Africa's largest livestock population (Deressa, 2007). Amongst the East African rangelands, the Borana rangeland management system in southern Ethiopia was regarded to be especially productive until the 1970s (Coppock, 1994). The Borana rangeland hosts about one million head of cattle, small ruminants and camels (CSA, 2015). Pastoralists used to achieve higher land productivity than extensive sedentary beef production (Cossins and Upton, 1987). However, in the recent decades, recurrent drought, woody plant encroachment, population increase, inappropriate rangeland management policies and land use change resulted in declining productivity of these rangelands (Dalle et al., 2009; Dida, 2011; Kamara et al., 2004). These changes have affected livestock production, which has been the major source of food and livelihood activities in the pastoral community in Borana (Coppock, 1994).

Mammalian herbivores play a crucial role in the sustainability of natural grasslands through their influence on the structural and functional properties of the ecosystem (Owen-smith, 1987). A certain threshold, i.e., the ecological carrying capacity, is assumed for each rangeland, below which the maximum number of animals on a given area of a land that can survive the greatest period of stress each year (Accatino et al., 2016). As soon as this carrying capacity is surpassed, the ecosystem´s balance and sustainability of a grazing regime can be disturbed (Chapin, 2009).

Carrying capacity of a rangeland is affected by rangeland vegetation productivity and quality (De Leeuw and Tothill, 1990; Köchy et al., 2008; Tietjen and Jeltsch, 2007), and climate change affects these two primary factors (Golodets et al., 2013). Quantifications of carrying capacities are difficult under the non-equilibrium concept (Roe, 1997). Particularly in rangeland areas of scarce and highly seasonal natural resources, capacities can highly vary across years (Roe, 1997; Treydte et al., 2001). While the concept of a stable carrying capacity is of limited utility for African conditions, the underlying principles on which it is based, are crucial for a sustained resource management (De Leeuw and Tothill, 1990). Recent advances in pastoral studies have not solved the stocking problem in African rangelands (Behnke and Kerven, 1994). The recommended management practice is the maintenance of conservative stocking rates, the equilibrium concept, which can be maintained in drier years, though considered as costly and inappropriate to pastoralists in a variable ecosystem (Vetter, 2005). To give management options, modeling the population sizes under different drought scenarios, combining the equilibrium and the non-equilibrium concepts, is important (Fig. 1.2), which includes the concept of a varying carrying capacity over time. In the semiarid rangelands such as the Borana rangelands no cattle population modeling has been conducted to encompass the variability of environmental resource that is dictated by rainfall, which would help exploring the economic outcomes of different stocking strategies (Vetter, 2005). We attempted such cattle population modeling to understand future trends and management options for the Boran cattle under climate change and varying carrying capacity scenarios.

1.3: The research gap and specific objectives

Several studies have tried to quantify biomass and carbon in woody vegetation (Ahmedin et al., 2013; Hasen-Yusuf et al., 2013; Montagnini and Nair, 2004). However, despite the apparent importance of grasslands for carbon sequestration (FAO, 2010), only few studies have tried to quantify the potential of grasslands under different grazing pressure, mainly in mesic grasslands, while such studies are completely lacking for semiarid tropical rangelands (Kramberger et al., 2014; McSherry and Ritchie, 2013; Piñeiro et al., 2010). Despite many studies on rangeland productivity, few studies have been investigating the complex interaction between herbivory and rainfall variability to acquire knowledge on the reaction and resilience of rangeland vegetation. As a reduction in net primary production leads to declined soil carbon stocks (FAO, 2010) improving forage production does not only improve the production of livestock system but also represents a low-cost way of mitigating climate change (Woomer, 2003). Therefore, this research was conducted to answer the following basic research questions:

- How do grass biomass, productivity and quality of two native grass species change under varying environmental conditions (grazing pressure, rainfall regime)?
- How does the Carbon storage and within plant allocation of the two native grass species change with increasing grazing frequency and decreasing rainfall amount?
- What are the main factors influencing cattle productivity in the Borana rangelands and how would the cattle population and its management change in the face of climate change?

The aim of this study was to experimentally determine the effects of herbivore pressure and changing rainfall regime on rangeland grass production and carbon storage and to translate this information to cattle population management.

Specific Objectives

1. To quantify how the nutrient quality (CP, ADF, NDF, ADL, TIVOMD) of the two study grass species (*C. ciliaris* and *C. gayana*) changes with increasing herbivore pressure
2. To test the above- and belowground grass biomass allocation under different herbivore pressure and rainfall amount.
3. To test the above- and belowground grass carbon storage under different herbivore pressure and rainfall amount.
4. To model the Boran cattle population based on verified data under different drought scenarios

Research Hypotheses

Our research hypotheses were

1. Under ambient average annual rainfall, we expect that there is an optimum clipping frequency, which leads to more aboveground production than other clipping frequencies. In contrast, belowground biomass will not be strongly affected by clipping treatment but rather by watering amount
2. Increased clipping frequencies will reduce aboveground biomass but less so belowground biomass and increase grass productivity (regrowth) under ambient rainfall regimes.
3. There is an optimum grazing frequency at ambient average annual rainfall that leads to highest overall (above- and belowground) biomass and carbon storage of grasses.
4. High grazing frequencies reduce the overall grass biomass, particularly in drought simulated condition.
5. In the face of climate change, the cattle population size reduces with increased drought frequency if no appropriate management regime is applied, i.e., early harvesting before drought hits the cattle population will be most beneficial focusing on males.

1.4: Outline of the thesis

This research focused on the experimental assessment of the rangeland grass biomass and carbon storage and how the allocations of these within the plant were affected by grazing pressure and rainfall variability. The main body of the research consists of controlled experiments of two native grass species under the influence of two major stressors: herbivore pressure and rainfall shortage (clipping and irrigation, respectively). These experiments were conducted on different spatial scales and in differently controlled environments, i.e., on a pot level in the lath house, in a field plot study and using moving cages in the field and observation techniques. The shift in response of differently aged individual grasses to clipping and irrigation provides helpful insights into the management of reseeded grassland for better biomass allocation and carbon storage in the face of climate change and increased grazing pressure. In general, the research outcomes presented in chapters 2 and 3 provide extensive answers for objectives 1, 2, and 3 of this study. For these, the aim was to experimentally determine the response in biomass, nutrition and carbon (C) as a result of grazing pressure and rainfall variability.

The study also used empirical data for stochastic models on the Boran cattle population dynamics under different drought scenarios. Objective 4 is concerned with the modeling of the Boran cattle population under drought frequencies based on empirical data collected from the Borana rangelands.

As a whole, the chapters of this thesis present outcomes of grass-herbivore interaction as well as the impacts of increased drought frequency on Boran cattle population size. Although each chapter provides novel and imperative results, it is only the combination of each chapter that can help understanding the effects of grazing and rainfall variability on the rangeland grass biomass, nutrient and carbon storage as well as varying carrying capacity on population size in the face of climate change. This information is necessary to develop a sound approach to rangeland management principles, which link the rangeland productivity (quality and quantity as well as carbon storage) to livestock population. Understanding such relationships among ecosystem elements contributes to the global climate change mitigation and adaptation strategies through enhancing the resilience of the rangeland ecosystem that leads to sustainable use of natural resources (Fig. 1.5) and food security.

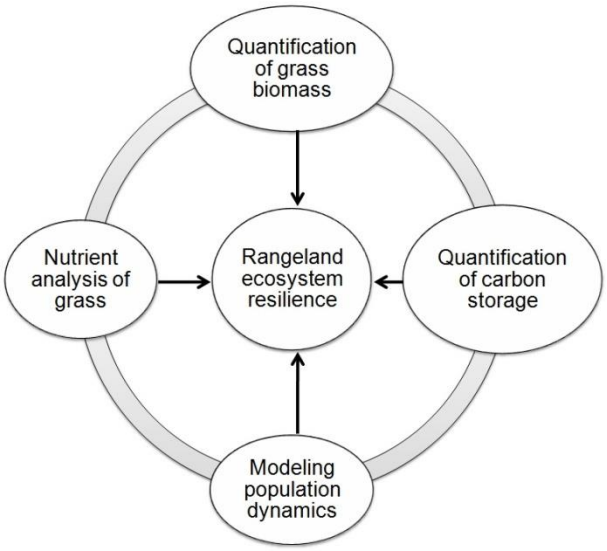

Figure 1.5 Schematic representation of different aims and methodologies used all together in the study.

Chapter 2: Clipping and irrigation enhance grass biomass and nutrients: implications for rangeland management*

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*A version of this chapter is published as:

Tuffa, S., Hoag, D. and Treydte, A.C., 2017. Clipping and irrigation enhance grass biomass and nutrients: Implications for rangeland management. Acta Oecologica, 81, pp.32-39, doi.org/10.1016/j.actao.2017.05.001. The original publication is available at: http://www.sciencedirect.com/science/article/pii/S1146609X16302521

Abstract

Increasing frequency of drought and high herbivore pressure significantly affect individual grass functions in semiarid regions. Reseeding of degraded rangelands by native grass species has been recommended as a tool for restoration semiarid rangelands. However, how grass species used for reseeding respond to stressors has not been fully explored. We examined biomass allocation and nutrient contents of *Cenchrus ciliaris* and *Chloris gayana* in the semiarid Borana rangelands, Ethiopia. We tested clipped mature tufts of the same species for biomass allocation and nutritive values. Further, shifts in rainfall and herbivory were simulated by three irrigation and four clipping treatments, respectively, for newly established grasses in pot and field plot experiments. Aboveground biomass (AG_B) significantly declined by up to 75% under increased clipping in mature tufts. In contrast, clipping significantly stimulated up to 152% higher AG_B of newly established grasses. Lower irrigation reduced the AG_B by 24 and 42% in *C. ciliaris* and in *C. gayana*, respectively. Clipping, further, significantly enhanced grass nutrients in grass tufts by up to 82 and 105% in *C. ciliaris* and *C. gayana*, respectively. Hence, management should focus on balancing this trade-off in mature grasses for nutritious rangeland production by clipping and storing for later supplemental feeding when grass nutrients drop. Further, young pastures should be moderately clipped/grazed for better establishment and biomass allocation.

Keywords: Borana rangelands, Crude protein, Ethiopia, Herbivory, Semiarid.

2.1: Introduction

Maintaining productivity of rangelands requires extensive knowledge on how vegetation responds to the dominant environmental factors such as grazing and climate variability. Rangelands across the world are facing increasing pressure due to overgrazing and climate change (Chimner and Welker, 2011); drought and herbivory are the primary savanna stressors (Baruch and Jackson, 2005). Particularly in eastern Africa, drought and overgrazing have led to deteriorated rangelands and a subsequent die-off of livestock populations after severe droughts (Catley et al., 2014). Generally, climatic stresses account for about 63% of all stressors on land degradation in Africa (Porto, 2014) while overgrazing causes 49% of soil degradation, mainly in semiarid and arid regions of Africa (WRI et al., 1992). Hence, sound management of rangelands including reducing livestock numbers (Abusuwar and Yahia, 2010; Zhang et al., 2015), letting the pasture vegetation recover (Angassa and Oba, 2010), and reseeding with perennial grasses (Mganga et al., 2011; Tebeje et al., 2014) is required. However, often, intensive management activities have been neglected as little is known on the resilience of the existing grass species and which grass species would be most suitable for reseeding (Mganga et al., 2013).

The effects of herbivory on biomass production have been controversial. Many findings indicated that herbage dry matter yield decreases with increasing herbivory (Kramberger et al., 2014; Yan et al., 2012) but Martin & Chambers (2001) claimed that clipping had no effect on total biomass. Yan et al. (2012), observed that rotational, i.e., moderate grazing reduced aboveground biomass and increased belowground biomass whereas Gao et al. (2008) observed a decrease of belowground biomass with increasing grazing intensity. Further, responses of reseeded grasses to grazing at different age class have rarely been compared under variable rainfall amount, which is a dominant driver that governs primary productivity (Schönbach et al., 2012).

In semiarid rangelands, 90% of plant productivity occurs belowground but grass root responses to clipping are not as well understood as shoot responses (Balogianni et al., 2014; Zhou et al., 2012) due to the difficulty of estimating belowground net primary productivity (Gao et al., 2008). Yet, to successfully manage rangelands under herbivore and climatic pressure, there is an urgent need to understand resource allocation of grasses in response to such stress factors. Up till now, little was known about how grazing and water availability interactively affect the native above- and belowground productivity of grass species in reseeded semiarid rangelands.

In addition to forage biomass, the determination of plant nutrient contents is fundamental for rangeland management (Arzani et al., 2012) as livestock production is limited by forage nutritional value (Ren et al., 2016). Thus, improvement in grass quality and quantity through reseeding with native, perennial grass species directly contributes to a sustainable cattle production (Homann et al., 2004). Cattle have been shown to select for high-quality grass (de Vries and Schippers, 1994), and under heavy grazing, it has been shown that dry matter digestibility has low values (Allison, 1985). In the Borana rangelands, not only grass quantity but also the quality of foraging sites showed significant spatiotemporal heterogeneity (Abebe et al., 2012a, 2012b; Keba et al., 2013; Teka et al., 2012). While it is known that grazing frequency greatly influences the nutritional value of grasses (Georgiadis and McNaughton, 1990), and thus, cattle production (Takele et al., 2014) empirical management recommendations are lacking particularly for Ethiopia's reseeded rangelands, which have paramount importance in protecting genetic erosion of the highly productive Boran breed (*Bos indicus*) (Homann et al., 2003).

Our experiments were aimed at resembling the two main pressures, herbivory and changes in rainfall regime, and their interactions in different intensities on two common rangeland grasses (*Cenchrus ciliaris* and *Chloris gayana*) in Ethiopian rangelands (Jorge et al., 2008). These grasses are widely used for reseeding (Tebeje et al., 2014) owing to their high digestibility and rapid growth (Angassa, 2005; Keba et al., 2013).

We aimed at answering the following research questions:

1. Will grazing influence both above- and belowground biomass of *C. ciliaris* and *C. gayana* similarly?
2. Will the two main rangeland grasses, *C. ciliaris* and *C. gayana*, vary in response to grazing at different ages?
3. What are the responses of grass biomass to increased or decreased irrigation amount?
4. Are the effects of clipping and irrigation interactive?
5. Will clipping decrease the digestibility and nutrient values of grasses?

2.2: Materials and methods

2.2.1: Study area

Our study area was located at Yabello Pastoral and Dryland Agriculture Research Centre (04°52'34"N and 038°08'48.0"E) in the Borana rangelands, southern Ethiopia. The annual rainfall of Yabello ranges from 327 to 1343 mm with a mean (± SD) of 645 (± 232) mm, and is bimodal with 52% of rain occurring during the main rainy season (from March to May) and 31% occurring during the short rainy season (from September to November). The mean annual temperature is 20°C with average maximum and minimum temperatures of 26 and 14°C, respectively (National Meteorological Agency and Yabello weather station, Pers. Comm.).

The Borana rangelands, which were once known for their outstanding rangeland management in Eastern Africa (Homann et al., 2003), are recently facing severe production problems. The rangelands' pasture vegetation has rapidly declined over the last decades due to increased cropping, bush encroachment, population increase and recurrent drought (Catley et al., 2014; Gemedo-Dalle et al., 2006). Consecutively, feed shortage has become the major challenge for animal production in the area (Tolera and Abebe, 2007). Reseeding of these grazing lands is recommended (Tebeje et al., 2014), and both *C. ciliaris* and *C. gayana* are native to the study area and highly suitable (Tefera et al., 2007).

2.2.2: Experimental layout

We tested grass regrowth in terms of aboveground biomass (AG_B) and belowground biomass (BG_B), across four levels of clipping frequencies (simulating herbivory) and three levels of irrigation (simulating rainfall regime) in the pot (1) and field plot (2) experiments. Further, we conducted a clipping experiment (3) under natural rainfall conditions during the rainy season on already established grass tufts of both *Cenchrus ciliaris* and *Chloris gayana* species in the field to test grass biomass and nutrient allocation. For pot and field plot experiments, seedlings were grown in a seedbed in a lath house and then transplanted to the pots and field plots. The seeds used

for seedling establishment were collected from the same locations where clipping experiments on the mature tufts were carried out.

Characteristics of the two study species are appropriate for the environmental conditions of our study area: *C. ciliaris* grows at an altitude below 2000 masl with more than 250 mm mean annual rainfall and can be found in areas of heavy grazing pressure (Mengistu, 2002). This species establishes well from seed and is suited for restoration of degraded areas. *Chloris gayana* is found at altitudes below 2400 masl with more than 600 mm annual mean rainfall, tolerating heavy grazing (Mengistu, 2002).

To evaluate biomass and nutrient allocation responses of already established study grass species to different clipping frequencies, we investigated mature individuals of *C. ciliaris* and *C. gayana* at locations where the grasses were found naturally under ambient rainfall conditions. We cut all grass tufts selected to an equal height of 10 cm, a height at which dry matter intake by livestock begins to decline (Chacon and Stobbs, 1976; Phillips, 2001), to have similar starting conditions. We considered tufts of equal circumferences in similar soil type located at least 1 m apart from each other (Cahill, 2003). We clipped 28 and 30 tufts *of C. ciliaris* and *C. gayana*, respectively, based on grass species dominance. Further, *C. ciliaris* was grazed by cattle of the research centre to test whether hand clipping and animal grazing had similar effects on grasses (Acharya et al., 2012). Hence, we erected cage enclosures around all grass tufts to exclude uncontrolled animal herbivory throughout the experimental period. Cattle were allowed to graze from the specific tufts by removing the cages every week at the same time with tufts of weekly clipping. The treatments were (i) frequent (weekly clipped), (ii) moderate (biweekly clipped) and (iii) none (unclipped), each replicated ten times. In *C. ciliaris*, we had one more treatment (iv) weekly grazing (grazing), all replicated seven times.

To understand responses of newly sown grass species to herbivory and rainfall we ran two factorial experiments simultaneously in experimental field plots and pots. The levels of clipping frequencies were (i) frequent (weekly clipped), (ii) moderate (biweekly clipped), (iii) light (monthly clipped), and (iv) none (unclipped/control). We increased irrigation based on a likely increase by about 5% in mean annual rainfall predicted for East Africa (CDKN, 2014; Christensen et al., 2007; Meehl et al., 2007). Accordingly, we varied the irrigation amount as (i) an increased mean annual rainfall by 5% ("higher"), (ii) average rainfall ("mean"), which was a long-term (30 years) average April, i.e., growing season, rainfall. The long-term (1984-2013) mean rainy days for April occurred for about 15 days in Yabello district, and we used these rainy days as irrigation frequency. We further used (iii) a lower overall amount: 70% of mean annual rainfall ("lower"), which has been shown to happen in drought years (Palchaudhuri and Biswas, 2013; Sheffield and Wood, 2008) that have become more frequent over the last years (He et al., 2014). The entire pot experiment comprised

72 pots (6 blocks x 3 irrigation x 4 clipping) per species. The pots were set up in the lath house in a 3 x 4 factorial experiment in a completely randomized block design. In the field plots, we set up a blocked design in factorial experiment following a similar layout to that of pot experiment, but with 7 blocks, and hence 84 field plots per species.

2.2.3: Data collection

We measured every regrowth with a ruler before each clipping event. All clipped parts were oven dried at 60°C for 48 hr (Adesogan et al., 2000; Holub et al., 2013). Each clipping was cumulated for AG_B per treatment. The sampling method was destructive (Tackenberg, 2007) and all grass roots were removed at the end of the experimental period to estimate BG_B per grass individuals (Jensen et al., 1990). We estimated BG_B by excavating all root parts, washing and filtering them through a 1 mm mesh size strainer before drying to a constant weight. Before analyzing AG_B and BG_B of mature tufts, we carefully standardized for initial sizes of all tufts, which were estimated by measuring the circumference of each tuft at the crown (Acharya et al., 2012).
We determined nutritional composition of mature grasses using Near-Infrared Reflectance Spectroscopy (NIRS) for CP, Ash, NDF, ADL, TIVOMD and ADF (Corson et al., 1999).

2.2.4: Data analysis

The AG_B, BG_B and nutritive values from mature tufts were subjected to one-way ANOVA with completely randomized block design to compare treatment effects, with irrigation and clipping as independent variables. Data generated from field plots and pots were analyzed for significant interaction by two-way ANOVA with the completely randomized block design. We used a significance level of $\alpha = 0.05$ with Fisher's least significant difference (LSD) test for significant main effects (clipping and irrigation) and Tukey's HSD test for significant interactions as post hoc test with GLM procedure of SAS (Littell et al., 2002). Analyses were done for each grass species separately and for each above- and belowground parts because species level response is essential for understanding community level response (Jobbágy and Sala, 2000). Data with non-normal residual distribution after Shapiro-Wilk test (Littell et al., 2002) were transformed before analysis.

2.3: Results

2.3.1: Aboveground biomass in mature tufts under clipping

The AG_B of mature *Cenchrus ciliaris* did not differ significantly across clipping treatments ($F_{(3,18)} = 1.81$, $p = 0.21$) but BG_B was 39% lower under no grazing compared to the other treatments ($F_{(3,18)} = 4.77$, $p = 0.013$; Fig. 2.1a). Weekly clipping resulted in BG_B similar to weekly grazing

values, highlighting that clipping resembles the effects of grazing very well. In *C. gayana*, frequent and moderate clipping significantly reduced AG_B by 75 and 66% ($F_{(2,18)} = 17.88$, $p < 0.0001$), respectively, whereas BG_B did not significantly differ ($F_{(2,12)} = 0.33$, $p = 0.73$; Fig. 2.1b).

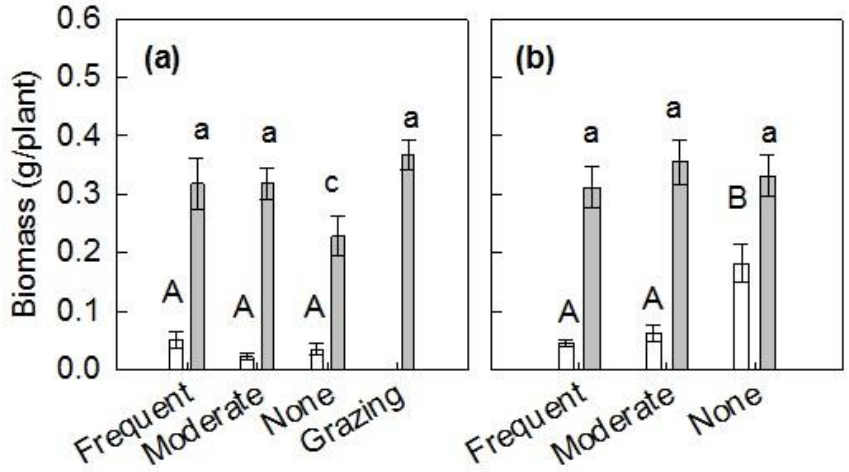

Figure 2.1 Mean (± SE) of aboveground (white bars) and belowground (gray bars) biomass (AG_B and BG_B, respectively) across clipping frequencies (frequent = weekly clipped, moderate = biweekly clipped, none = unclipped/control, grazing = weekly clipped) of (a) mature C. ciliaris and (b) mature C. gayana tufts. Different letters denounce significant difference across clipping frequencies.

2.3.2: Aboveground biomass in newly established grasses under clipping

Clipping significantly increased AG_B ($F_{(3,61)} = 4.21$, $p = 0.009$) of *C. ciliaris* but only slightly increased BG_B ($F_{(3,61)} = 3.02$, $p = 0.037$; Fig. 2.2a) compared to no clipping in pots. In field plots, moderate and light clipping significantly increased ($F_{(3,72)} = 5.41$, $p = 0.0021$) AG_B by 24 and 17%, respectively (Fig. 2.2b), while frequent and no clipping led to lowest AG_B allocation.

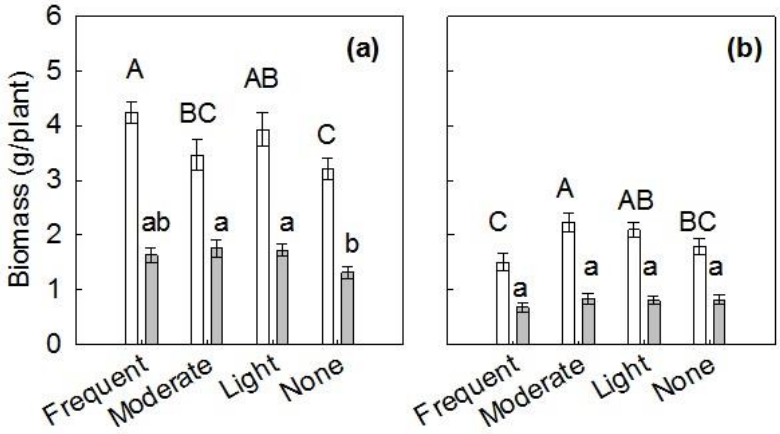

Figure 2.2 Mean (± SE) aboveground (white bars) and belowground (gray bars) biomass (AGB and BGB, respectively) across clipping frequencies (frequent = weekly clipped, moderate = biweekly clipped, light = monthly clipped, none = unclipped/control) of C. ciliaris in (a) the pot experiment and (b) the field plot experiment. Means in white bars followed by different upper case letters are significantly different. Means in gray bars followed by different lower case letters are significantly different across treatments.

2.3.3: Biomass allocation in grasses under irrigation

The lower irrigation amount significantly reduced AG_B in both *C. ciliaris* ($F_{(2,61)}$ = 8.49, p = 0.0006; Fig. 2.3a) and in *C. gayana* ($F_{(2,61)}$ = 15.03, $p < 0.0001$; Fig 2.3b) in the pot experiment. Further, this irrigation decrease also significantly reduced BG_B in *C. ciliaris* ($F_{(2,61)}$ = 9.55, p = 0.0002) and *C. gayana* ($F_{(2,55)}$ = 24.01, $p < 0.0001$) (Figs. 2.3a & 2.4a, respectively) while a slight increase in irrigation amount did not have additionally positive effects on AG_B or BG_B.

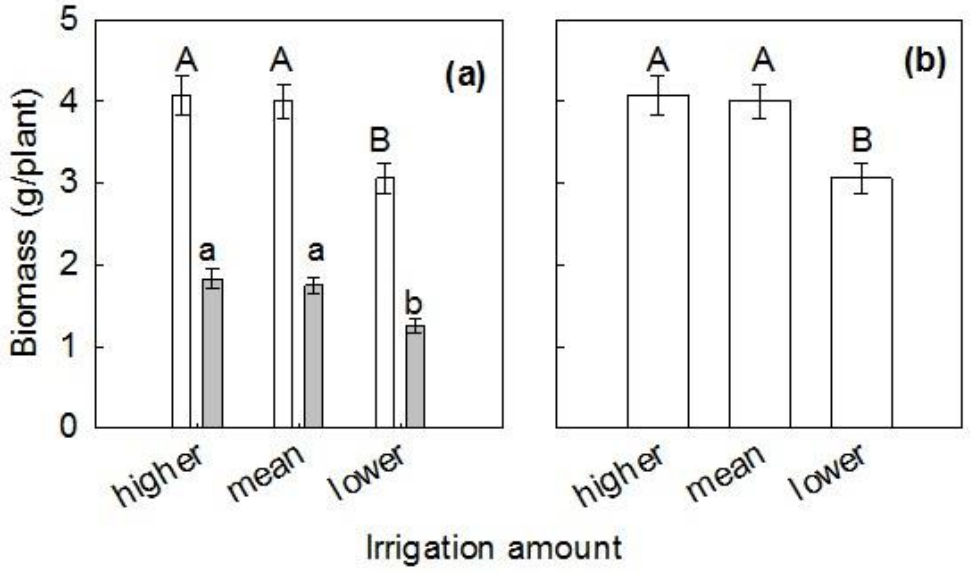

Figure 2.3 Mean (± SE) aboveground (white bars) and belowground (gray bars) biomass (AG_B and BG_B, respectively) across irrigation amounts (higher = 5% above average ambient rainfall, mean = ambient average annual rainfall, lower = 70% of average ambient rainfall) of **(a)** *C. ciliaris* and **(b)** mean (± SE) AG_B of *C. gayana* in the pot experiment. In the latter figure, we omitted the BG_B to avoid the ambiguity of presenting the same data twice since we present it in Fig. 2.4a as an interactive factor. Different letters denounce significant difference across treatments.

2.3.4: The interactive effects of clipping and irrigation on biomass

In pots, clipping and irrigation interactions were significant only for the BG_B ($F_{(6,55)}$ = 24.01; p = 0.023; Fig. 2.4a) but not for AG_B ($F_{(6,55)}$ = 2.18; p = 0.059) of *C. gayana*. Under light and no clipping, the higher irrigation significantly increased BG_B while decreased irrigation kept the BG_B significantly low at all clipping treatments (Fig 2.4a).

Clipping on its own led to significant differences in AG_B ($F_{(3,61)}$ = 14.03, $p < 0.0001$) and BG_B ($F_{(3,61)}$ = 3.42, p = 0.022) in the field plot experiment while irrigation amount alone did not ($F_{(2,72)}$ = 2.92, p = 0.06; $F_{(2,72)}$ = 1.12, p = 0.33, respectively). In the field plot experiment, the AG_B of C. gayana was by 127 and 152% significantly higher under moderate and light clipping, respectively (Fig. 2.4b).

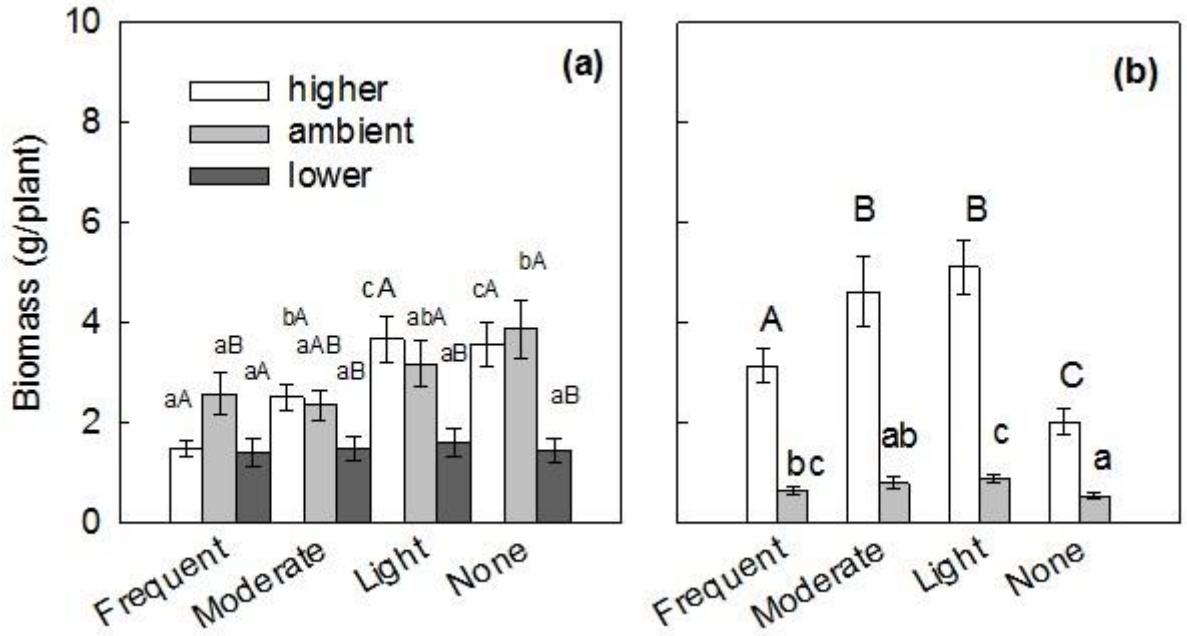

Figure 2.4 (a) Interactive effect of clipping (frequent = weekly clipped, moderate = biweekly clipped, light = monthly clipped, none = unclipped/control) and irrigation (higher = 5% above average ambient rainfall, mean = ambient average annual rainfall, lower = 70% of average ambient rainfall) on belowground biomass (BGB) of C. gayana in the pot experiment. Bar graphs with whiskers represent mean (± SE) BG_B across clipping frequencies and irrigation amounts. **(b)** Mean (± SE) aboveground (white bars) and belowground (gray bars) biomass (AG_B and BG_B, respectively) of *C. gayana* across clipping frequencies in the field plot experiment. Means of bars followed by different letters are significantly different

2.3.5: Nutritive values of mature tufts under clipping

The nutritive values of the two study species showed similar patterns across our treatments. Clipping significantly increased CP, TIVOMD and ADF contents (Fig. 2.5c, e, & f, respectively) while crude ash significantly decreased with increased clipping (Fig. 2.5b). The ADL significantly decreased with increasing clipping frequencies in *C. ciliaris* (Fig 2.5d) but not in *C. gayana*.

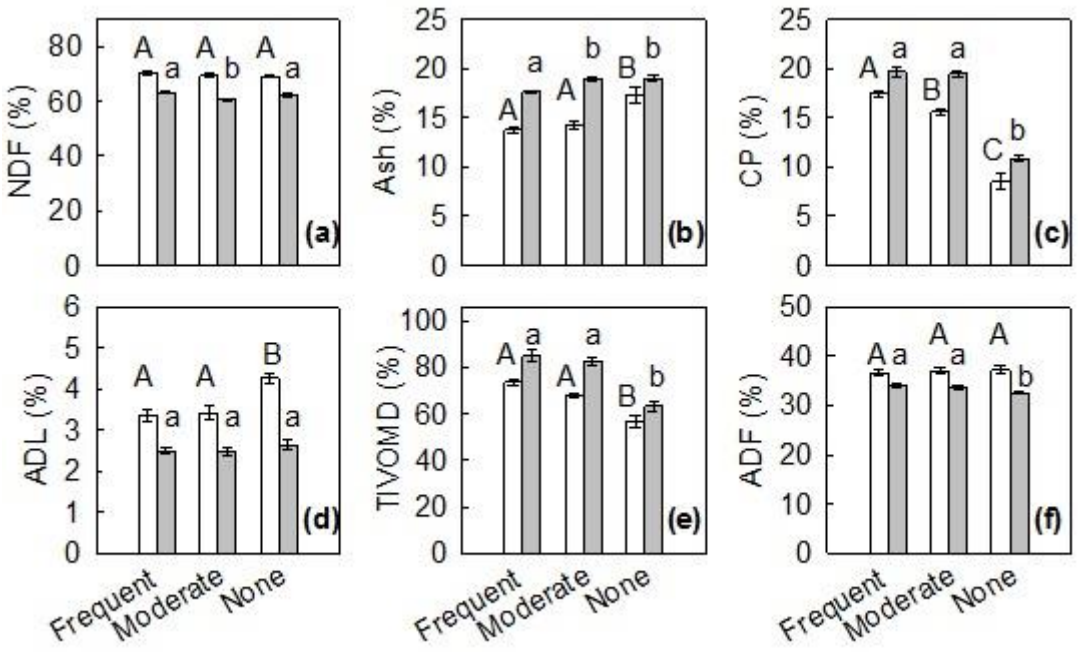

Figure 2.5 Percentage (± SE) nutritive values (NDF, Ash, CP, ADL, TIVOMD and ADF; **(a)** – **(f)**, respectively) in dry matter of *C. gayana* (white bars) and C. ciliaris (gray bars) across clipping frequencies (frequent = weekly clipped, moderate = biweekly clipped, none = unclipped/control). Means followed by different letters are significantly different across treatments. CP = crude protein, Ash = Ash value, NDF = neutral detergent fiber, ADL = acid detergent lignin, TIVOMD = true in-vitro organic matter digestibility and ADF = acid detergent fiber

2.4: Discussion

2.4.1: Aboveground biomass in mature tufts under clipping

The significantly reduced aboveground biomass (AG_B) of mature *Cenchrus ciliaris* and *Chloris gayana* under clipping was mainly caused by the removal of photosynthetic tissues, which was also reported by others (Bai et al., 2015; Gilbert and Fraser, 2013; Leriche et al., 2003; Shahzad et al., 2012). On the other hand, the enhanced belowground biomass (BG_B) under clipping and grazing compared to the unclipped control is in accordance with reports that grazing exclusion leads to reduced BG_B, which might be attributed to a lower demand of nutrients for growth under no defoliation (Shi et al., 2013; Stevens and Gowing, 2014). As such, reduced root growth reduces grass ability to compete for available water and nutrients (Engel et al., 1998) and, hence, becomes a survival challenge for grasses during drought (Hoogenboom et al., 1987). Therefore, grazing is an important factor for increasing belowground biomass and , thus, forage resources, which further increases grassland ecosystem services such as carbon sequestration (Larreguy et al., 2014). We found that grazing and clipping had a similar effect on biomass allocations, suggesting that clipping can be used as a proxy to identify grazing pressure effects on vegetation (Cuykendall and Marten, 1968). This result has paramount importance because the responses of dominant mature

grass species help to understand ecosystem resilience in the face of climate change (Nippert et al., 2009).

2.4.2: Aboveground biomass in newly established grasses under clipping

The higher AG_B under moderate clipping frequencies compared to non-clipping highlights that controlled grazing can strongly enhance biomass in a newly established pasture. This might be attributed to the fact that plants have the capacity to compensate or even overcompensate for herbivory at low levels of grazing pressure (Mei et al., 2014; Veen et al., 2014).

The freshly reseeded grasses reacted more strongly with enhanced production to defoliation than already established grasses, which might be due to the high photosynthetic capability of young leaves (Nowak and Caldwell, 1984). In contrast experiments using *Holcus lanatus* and *Lolium perenne* grasses showed that clipping stimulated older grasses more strongly than younger ones in producing clonal propagation (Aarssen and Turkington, 1987), which might be species specific artifact. Our findings have a paramount importance in the management of rangelands of different ages in areas such as Borana rangelands, where our study a species have recently been recommended for reseeding activities (Tebeje et al., 2014).

2.4.3: Biomass allocation in grasses under irrigation

The decreased irrigation reducing AG_B and BG_B of both grass species in our pot experiments showed that rainfall plays an overriding role in dictating productivity of grasses in semiarid environments. A 30% lower rainfall regime, a trend predicted for eastern Africa in the future climate change scenarios (Sheffield and Wood, 2008), would, therefore, lead to a 31 and 40% lower AG_B and BG_B, respectively, as water stress leads to reduced daily leaf extension (Busso and Richards, 1993). This result implies that under drought conditions grazing seems less important for grass productivity (Muthoni et al., 2014; Xu et al., 2013). Irrigation effects were not significant for both grass species in the field plot experiment. This might be attributed to potential horizontal and vertical seepages of water out of the field plots (Ochoa et al., 2009), which were not an artifact in the pot experiments.

2.4.4: Interactive effects of clipping and irrigation on biomass

The significant interactions between clipping and irrigation for BG_B suggested that low grazing pressure can enhance BG_B under mean or high rainfall, but not under low rainfall conditions, as reported by others in ecosystems of the Sahel (Le Houerou, 1989). These changes might be attributed to morphological, physiological and biochemical changes in moisture-stressed plants,

resulting from reduced CO_2 assimilation rates due to low stomatal conductance (Anjum et al., 2011). Further, a high BG_B of *C. gayana* at high rainfall in unclipped compared to clipped treatments indicated that under controlled grazing high rainfall can greatly enhance grass productivity. This might be an opportunity for some east African regions, where higher rainfall is predicted under the future climate change scenarios (Christensen et al., 2007). An increase in BG_B under clipping and irrigation combined at light and no clipping and a reduction under frequent and moderate-clipping might be attributed to slow elongation and decreased production of new roots (McInenly et al., 2010) as well as a reduced leaf extension rate due to water stress and biomass removal (Busso and Richards, 1993). Future grazing management should consider resting times of grazing areas for better biomass allocation and grass survival as BG_B plays a significant role in the long-term sustainability of rangelands (Engel et al., 1998; Hoogenboom et al., 1987). With our experiments that combined above- and belowground biomass allocation as grass species responses to herbivory are useful in order to understand grazing land ecosystem functions and resilience (Bardgett and Wardle, 2003). Restoration of degraded rangelands with perennial grasses plays an increasingly important role in rangeland sustainability (Christensen et al., 2005; Haddad et al., 2015; Mapfumo et al., 2002). Particularly, lowlands (highly productive areas and fallback pockets), which can potentially maintain the entire semiarid rangeland production system will require sufficient grass supply (Scoones, 1995). This supply could be a combination of reseeded and mature perennial grasses. While it has already been established that cropping of staple food is unsustainable in rangeland systems (Angassa and Oba, 2008; Solomon et al., 2007), some still support cultivation (Ng'ang'a et al., 2016), which is, under current and future climatic conditions, prone to frequent crop failure (Tache and Oba, 2010; Tolera and Abebe, 2007). This current trend of cultivating lowlands (Ng'ang'a et al., 2016) will lead to an extinction of important perennial grasses (Angassa and Oba, 2010; Solomon et al., 2007) and will, consecutively, undermine the resilience of rangelands (Elias et al., 2015).

2.4.5: Nutritive values of mature tufts under clipping

The main feed resource of Boran cattle (*Bos indicus*), which is the most important livestock species in the region (Zander et al., 2009b), is a natural pasture that shows seasonal variability not only in quantity but also in quality (Tolera and Abebe, 2007). In the Borana rangelands, grass species such as *C. ciliaris*, which has been ranked first as preferred cattle forage species by pastoralists (Keba et al., 2013), is decreasing at an alarming rate (Angassa, 2014). While it is possible to reserve grass as standing hay in enclosures (Angassa and Oba, 2010) the quality of grasses drops significantly during dry seasons (Abebe et al., 2012a, 2012b; Keba et al., 2013). However, compared to other local grass species (such as *Leptochloa fusca*, *Cynodon dactylon* and *Panicum*

colunum), *C. ciliaris C. gayana* have higher nutritive values with low ash contents (Sultan et al., 2011). Our results, which were within the range of the study species (Abebe et al., 2012b; Keba et al., 2013), clearly indicated that clipping can significantly increase grass nutrient quality in both *C. gayana* and *C. ciliaris*. Clipping decreased the ash content by 20 and 7% while it increased CP content by 105 and 82% in *C. gayana* and *C. ciliaris*, respectively. Similar findings were reported by other researchers for grazing and clipping in the same as well as other species (Georgiadis and McNaughton, 1990; Leriche et al., 2003; Pavlů et al., 2006). Clipping also improved the true in vitro organic matter digestibility (TIVOMD) by 31 and 34% in *C. gayana* and *C. ciliaris*, respectively. Therefore, we recommend that grasses should be clipped and stored for dry season or drought period supplementation, for instance, by the cut-and-carry principle or put-and-take stocking during their growth periods (Allen et al., 2011; Mekuria, 2013) to fortify the deficient forage. This can be done at an exclosure level, *Kalo* (Lind et al., 2016), which can provide nutritious feed for calves and attenuated cattle during the dry season or drought.

Grasses should be cut while still growing for better nutritional quality rather than waiting until maturity, the latter being a common practice in the Borana rangelands. Further, our two study grass species not only occur in Borana but also in rangelands across the world; for instance, *C. ciliaris* is the only cultivated grass in its area of origin and of potential application in other climate zones while *C. gayana* is the most important cultivated tropical grass of today (Boonman, 1993; Marshall et al., 2012). Hence, understanding their resilience towards drought and herbivore pressure has global implications.

2.5: Conclusion

Our findings provide important information for local decision makers, which might enhance the establishment and management of reseeded areas in the Borana rangelands. However, future experiments should cover long-term studies to clarify the potential of those grass species that proved to be promising within our study. The results from this study will greatly increase the available information on above- and belowground production in *C. ciliaris* and *C. gayana*. Our results very likely could be used to manage restored sites in other semiarid ecosystems reseeded by grasses of the same species. We recommend that the traditional way of pastoralism, including resting places that exclude grazing (*Kalos*), should be supported; and that new management alternative such as reseeding should be further explored with other potential grasses to prove if there are species-to-species differences between grasses used.

Chapter 3: Effects of clipping and irrigation on carbon storage in grasses: implications for CO_2 emission mitigation in the rangelands*

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* A version of this chapter has been submitted to Carbon Management on 04 January 2017 as:

Tuffa, S., Hoag, D. and Treydte, A.C. Effects of clipping and irrigation on carbon storage in grasses: implications for CO_2 emission mitigation in the rangelands

Abstract

Increase in drought frequencies and herbivore pressure strongly affect grass carbon storage in semi-arid rangelands. However, understanding how individual grasses respond to herbivory and rainfall has been hampered by the difficulty of quantifying above- and belowground carbon (C) storage in grasses. Particularly by restoring degraded rangelands through reseeding, their C storage potential can be greatly enhanced. We assessed the responses of reseeded grasses to the effect of herbivory and precipitation to evaluate the potential of individual grasses for C storage as a technique for climate change mitigation. We conducted clipping experiments on mature grass tufts of two native grass species, *Chloris gayana,* and *Cenchrus ciliaris,* in the semi-arid Borana rangelands, Ethiopia. Further, we experimentally quantified above- and belowground C storage of young grasses of the same species in pot and field plot trials under simulated grazing and variable rainfall. Our results showed that aboveground C was significantly four times lower in the clipped compared to unclipped mature grasses. In contrast, three times higher C was found in young reseeded grasses that were clipped compared to unclipped ones. Clipping and irrigation in combination significantly influenced belowground C in young grasses, with reduced irrigation overriding clipping effects. We conclude that a moderate grazing should be encouraged to enhance CO_2 uptake, consequently contributing to climate change mitigation in rangelands.

Key words: Borana, Herbaceous layer restoration, Herbivory, Livestock management, Rainfall variability.

3.1: Introduction

Carbon dioxide (CO_2), the most abundant anthropogenic greenhouse gas, is a driving factor in climate change, which increased by 40% from a pre-industrial value in the year 1750 of about 280 ppm to 391 ppm in 2011 (IPCC, 2013, 2007). Put differently, if we take in our next breath, we will be breathing in 40% more CO_2 than if we were breathing in 1975. Carbon storage in degraded semi-arid rangelands by improved land management methods, such as reseeding with native grass species, is assumed to contribute substantially to climate change mitigation (Gifford, 2010). In Borana rangelands, southern Ethiopia, native grass species are reseeded to restore degraded rangeland areas thus increasing forage production (Tebeje et al., 2014). Grasslands can provide a significant C storage in semi-arid environments (Wang et al., 2011). However, a grasslands' ability to store a large amount of C is primarily controlled by two environmental stressors - herbivory and precipitation (Chimner and Welker, 2011). Herbivory removes aboveground biomass and changes the belowground biomass and, hence, C storage in rangelands (Derner et al., 2006). Carbon storage

decreases and barely recovers under heavy grazing (Wang and Batkhishig, 2014); but moderate to heavy grazing can also increase root biomass (Larreguy et al., 2014) and, hence, higher overall plant C storage (Hafner et al., 2012) in the long run. Little is known about the regrowth response of plants to herbivory (Falk et al., 2014) that influences the C storing capacity of grasses.

In the Borana rangelands, two perennial C_4 grass species (*Cenchrus ciliaris* and *Chloris gayana*) are particularly important because they are highly palatable, native species and are being used to reseed degraded grazing land (Tebeje et al., 2014). Such managements can also increase C storage which has paramount importance in the face of climate change (Thomey et al., 2014). With suitable management practices, considerable increases in C storage or decreases in C losses and greenhouse gas emissions can be achieved (Tennigkeit and Wilkes, 2008). However, the response of these grasses to grazing frequency, under variable rainfall amount after reseeding remains unknown. Hence, in this study, we aimed at estimating the carbon storage of the two native C_4 grasses under grazing and rainfall regime by simulated clipping and irrigation, respectively.

Roots are the major carbon source in the soil (Snyman and du Preez, 2005) and such a management approach with an objective of forage production as a co-benefit may promote mitigation activities (Milne et al., 2016). Few studies focused on the role of grasslands as a C storage in their belowground biomass component (Frank et al., 2004).

Climate change will result in multiple stresses for plants and animals in the coming decades. Both amounts of heavy precipitation and intensity of drought are likely to increase in the future due to climate change (IPCC, 2013). Drought suppresses plant productivity (Xu et al., 2013) and will diminish recovery potential of overgrazed rangelands (Busso and Richards, 1993). Large uncertainties exist regarding the C storage factors under different climate regimes and management systems of grasslands in general (Petri et al., 2010). Little is understood about the effects of combinations of climate and herbivory-related stressors on the C storage of grasses (Campbell and Stafford Smith, 2000). In this study, we focused on responses of grasses to the clipping and grazing in allocating their carbon storage.

In southern Ethiopia, rainfall is predicted to be lower with future climate change (Funk et al., 2014). Based on the annual rainfall data, rainfall strongly varies with above- and below-average rainfall (Mwangi et al., 2014) and, hence, we resembled this variation in our irrigation treatments. We combined rainfall variability and grazing pressure to acquire knowledge on C storage of grasses, particularly in reseeded species. Information generated from such experiments will help in designing appropriate management of newly reseeded grasslands that enhance their ecosystem service such as C storage in the face of climate change.

The objectives of this study were to (i) quantify the effects of clipping on the C storage in mature and young grasses, (ii) assess the interactive effects of grazing and rainfall variability on the two

native grass species in Borana rangelands of South Ethiopia. We addressed the following questions/hypotheses:

1. How do clipping frequencies influence grass C storage in above- and belowground parts?

2. What are the responses of grass C to increased or decreased irrigation?

3. Are effects of clipping and irrigation interactive?

4. What are the implications for C storage, in the face of climate change, of the study grass species in the Borana rangelands?

3.2: Materials and methods

3.2.1: Study site

Our experiments were conducted in the Borana zone, at the rangeland research station of Yabello Pastoral and Dryland Agriculture Research Centre (N04°52', E038°08'; 1626 masl), southern Ethiopia. The rainfall of Yabello ranges from 327 to 1343 mm per annum with mean annual rainfall (± SD) of 645 (± 232) mm (National Meteorological Agency and Yabello weather station, Pers. Comm.). It is bimodal with 52% of rain occurring during the main rainy season (from March to May), and 31% occurring during the short rainy season (from September to November). The mean annual temperature is 20°C with average maximum and minimum temperatures of 26°C and 14°C, respectively (National Meteorological Agency and Yabello weather station, Pers. Comm.).

We conducted two separate experiments on two native grass species, *C. ciliaris* and *C. gayana*, in the Borana rangelands. We ran the first experiment on already established mature tufts under natural rainfall conditions during the main rainy season. For both species, we used different clipping frequencies to simulate grazing pressure. Further, we applied clipping and irrigation on newly established grasses in pots and field plots from November 2013 to February 2014, i.e., during the dry season.

3.2.2: The mature tufts clipping experimental design

In the first experiment, we selected in total 58 tufts of two mature grass species (*C. ciliaris* and *C. gayana*) of similar size. The two sites were less than 500 m apart from each other and, hence, environmental conditions were assumed to be similar. During tuft selection, we considered independent, individual tufts within 5m distance from each other. In addition, circumferences of all tufts were measured at their base prior to clipping and tufts of similar size were used and hence differences in tuft sizes were ignored. Between April and June 2013, both species were subjected

to a completely randomized block design with different clipping frequencies, i.e., we erected 28 cages above *C. ciliaris* tufts in seven replications; we used three clipping frequencies to simulate grazing pressure (weekly clipping = "frequent", biweekly clipping = "moderate", and no clipping = "control"). Moreover, we measured the belowground biomass of tufts, in seven replications, where cattle were allowed to graze on a weekly basis (= "grazing"), adjacent to the cages for clipping frequencies, to record differences in response to grazing and clipping. Animals were taken directly to the experimental site before they access other feed so that they graze on the dominant tufts, i.e., *C. ciliaris*, without making any selection. We also observed that cattle preferred *C. ciliaris* which had been already recognized as palatable (Keba et al., 2013). For the second species, *C. gayana*, we used three clipping frequencies (frequent, moderate and control) with ten replications each. For the latter species, we did not use cages because the area was completely fenced off from any domestic and wild grazers; but grasses had been hand clipped for hay making since 2008.

3.2.3: The combined clipping and irrigation design

For the second experiment of pots and field plots, we collected rainwater in plastic water storage tanks during the rainy season and used it for dry season irrigation as a second factor, in addition to clipping frequencies (frequent = weekly clipped, moderate = biweekly clipped, light = monthly clipped, control = unclipped). We ran the pot and field plot experiments simultaneously during the dry season, with the assumption that C stored in grasses is primarily controlled by two environmental stressors - herbivory and precipitation (Chimner and Welker, 2011).

Irrigation resembled the condition of a typically wet April, the main growing season of our two focus grass species (Angassa, 2005). The April average rainfall (158.8 mm) of 30 years (1984-2013) was divided by the average number of rainy days (~15 days over 30 years) to get April rainfall amount per event that we used to calculate volume of water that we added as average rainfall (= "ambient") treatment; we derived from the ambient treatment scenarios of a 5% rainfall increase (= "higher") and a 30% rainfall decrease (= "lower") treatments. We calculated the irrigation amount as, volume = water depth (daily April rainfall) x surface area (of field plot or pot). The irrigation treatments were hand watered every other day throughout the experimental period.

Before starting the experiments, grass seedlings of both species were raised on a seedbed in a lath house and transplanted into pots and field plots. We transplanted one seedling of the same size per pot and per field plot. In total, we transplanted 72 and 84 individual seedlings to pots and field plots, respectively, per species. Seeds used in the seedling establishment for pot and field plot experiments were collected in the previous years from the same site (i.e., within a radius of ½ km

around the study site of mature tufts). Hence, we assumed that the seeds used for pot and field plot experiments were genetically similar to the mature tufts that we used during the rainy season experiment.

In the field plots, we carefully drilled holes with 5 cm diameter using a motorized soil auger to a depth of 10 cm for seedling transplanting without disturbing neighboring soil structure. In the pots and field plots, both grass species were subjected to a factorial experiment with randomized complete block design of four clipping frequencies (frequent, moderate, light and control) and three irrigation amounts (higher, ambient, and lower). All experimental procedures were the same for field plot and pot experiments except the number of blocks, which were 7 and 6, respectively. The soils for pots experiment were collected from the same site where we conducted the field plot experiments. Soils of each block for pot experiment were mixed and sieved before the experiment to remove roots and other debris and mixed again to increase homogeneity within a block. Hence, we assumed all belowground plant materials that we harvested at the end of the experiments were from the present growth only.

3.2.4: Above- and belowground biomass collections

Before commencing the treatments, all grass tufts were clipped to have similar starting conditions at a recommended height of 10 cm that mimics optimal grazing height (Bryan et al., 2000; Phillips, 2001), which was kept throughout the experiments. We oven dried the clippings at a recommended temperature of 60°C for 48 hours before weighing (Adesogan et al., 2000). At the end of the experiments, weights of the clippings were summed per clipping to obtain the total weight of individual grasses.

We excavated all the 370 roots at the end of the experiments because excavation was suggested for enabling total amount of root comparison (Atkinson and Dawson, 2001); i.e., we excavated roots of the 58 mature tufts by digging a 100 cm wide hole to 100 cm depth; we also excavated all 168 roots of both study grass species from the field plot experiment, by digging a 50 cm wide hole to 50 cm depth. We collected all roots with soil and soaked in water, washed and strained through small mesh sized sieve (1 mm) to remove fine roots from soils. We harvested, from the pot experiment, the 144 roots by soaking the entire soil from the pots in water and washing through a sieve. The washed roots were then oven dried at 60°C for 48 hrs (Adesogan et al., 2000).

Then, the C content of above- and belowground biomass of the study grass species was calculated based on the comprehensive standard that the C content of most plant tissue is in the range of 45-50% (Schlesinger, 1991). Therefore, the coefficient of 0.475 was used on average for calculating C storage in above- and belowground biomass.

3.2.5: Statistical Analysis

We analyzed the above- and belowground C of mature tufts by one-way analysis of variance (ANOVA) with completely randomized block design while data from field plots and pots were analyzed for significant interaction by two-way ANOVA with completely randomized block design at a significance level of $\alpha = 0.05$. We used Fisher's least significant difference (LSD) test for significant main effects (clipping and irrigation) and Tukey's HSD test for significant interactions as post hoc test with GLM procedure in SAS (Littell et al., 2002). Analyses were done not only for each grass species separately in each experiment but also for each above- and belowground part in all experiments. We transformed data with non-normal residual distribution after Shapiro-Wilk test using square root, log, and inverse transformation.

3.3: Results

3.3.1: Responses of carbon to clipping frequency in mature grass tufts

Weekly grazing, frequent and moderate clipping significantly improved the bgC of *C. ciliaris* ($F_{(2,12)} = 4.61$; $P = 0.0146$) compared to no clipping. The difference between grazing and clipping was non-significant (Fig. 3.1a).

Aboveground OC was significantly higher in the unclipped compared to the clipped treatments in already established tufts of *C. gayana* (Fig. 3.1b). There was no significant difference among the treatments for the bgC storage ($F_{(2,18)} = 0.33$; $P = 0.7254$; Fig. 3.1b).

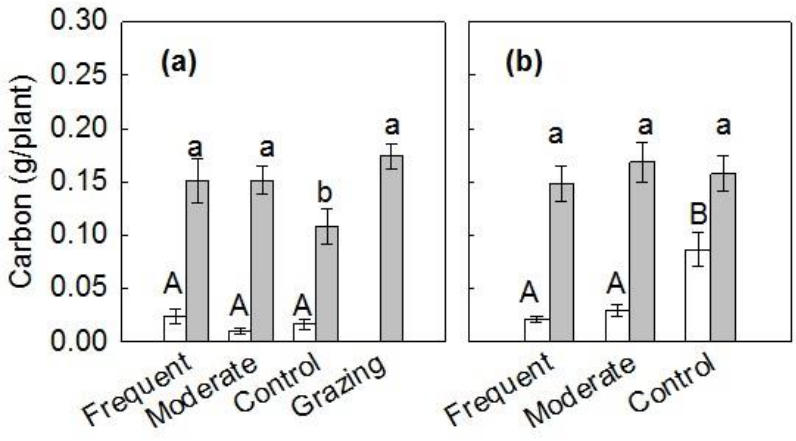

Figure 3.1 (a) Mean (± SE) of above- (white bars) and belowground (gray bars) C of C. ciliaris across clipping (frequent = weekly clipped, moderate = biweekly clipped, none = unclipped/control, grazing = weekly grazed). **(b)** Mean (± SE) of above- and belowground C of *C. gayana* tufts across clipping frequencies (frequent, moderate and control). Different letters denounce significant difference across clipping frequencies by LSD test.

3.3.2: Clipping and grass carbon storage in newly established grasses

In the field plot experiment, moderate and light clipping significantly improved the agC of *C. ciliaris* (F(3,72) = 5.41; P = 0.0021; Fig. 3.2a) and *C. gayana* (F(3,72) = 14.03; P < 0.0001; Fig. 3.3b) compared to frequent and no clipping. The clipping effects for bgC of *C. ciliaris* did not show significant differences ($F_{(3,72)}$ = 0.76; P = 0.5229; Fig. 3.2a). In pot experiment of *C. ciliaris*, unlike the field plot experiment, bgC showed significant reduction in the control ($F_{(3,61)}$ = 3.01; P = 0.0367; Fig. 3.2b).

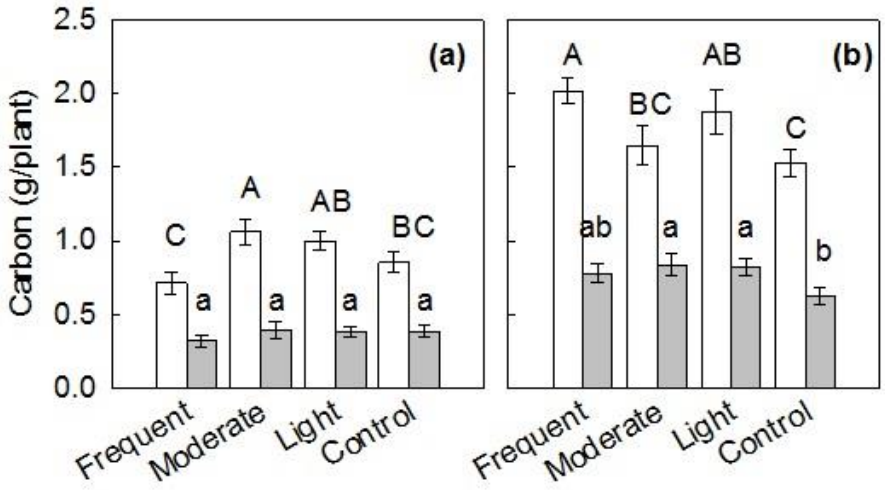

Figure 3.2 (a) Mean (± SE) above- (white bars) and belowground (gray bars) C of *C. ciliaris* across clipping frequencies **(**frequent = weekly clipped, moderate = biweekly clipped, light = monthly clipped, none = unclipped/control) in the field plots experiment. **(b)** Mean (± SE) above- and belowground C of *C. ciliaris* across clipping frequencies (frequent, moderate, light, and control) in the pot experiment.

In field plot experiment, bgC of *C. gayana* was significantly higher ($F_{(3,72)}$ = 3.42; P = 0.0218; Fig. 3.3b) under moderate and light clipping than under the two extreme treatments, frequent and no clipping. The effect of clipping was not significant for the agC of *C. gayana* ($F_{(3,61)}$ = 0.17; P = 0.915; data not shown) in pot experiment.

3.3.3: Combined effects of clipping and irrigation

There were significant interactions between clipping and irrigation for bgC only in *C. gayana* ($F_{(6,55)}$ = 2.68; P = 0.0235; Fig. 3.3a) and no significant interactions were observed for agC of *C. gayana* ($F_{(6,55)}$ = 0.82; P = 0.5573 and $F_{(6,55)}$ = 2.18, P = 0.0584) and *C. ciliaris* ($F_{(6,55)}$ = 1.18, P = 0.3261 and $F_{(6,55)}$ = 0.50; P = 0.8037) and bgC of *C. ciliaris* ($F_{(6,66)}$ = 0.77, P = 0.5994 and $F_{(6,55)}$ = 1.19; P = 0.3234) in both field plots and pots experiments, respectively. At lower clipping frequencies the bgC significantly improved under increased irrigation amount, but at decreased irrigation amount, clipping did not enhance bgC (Fig. 3.3a).

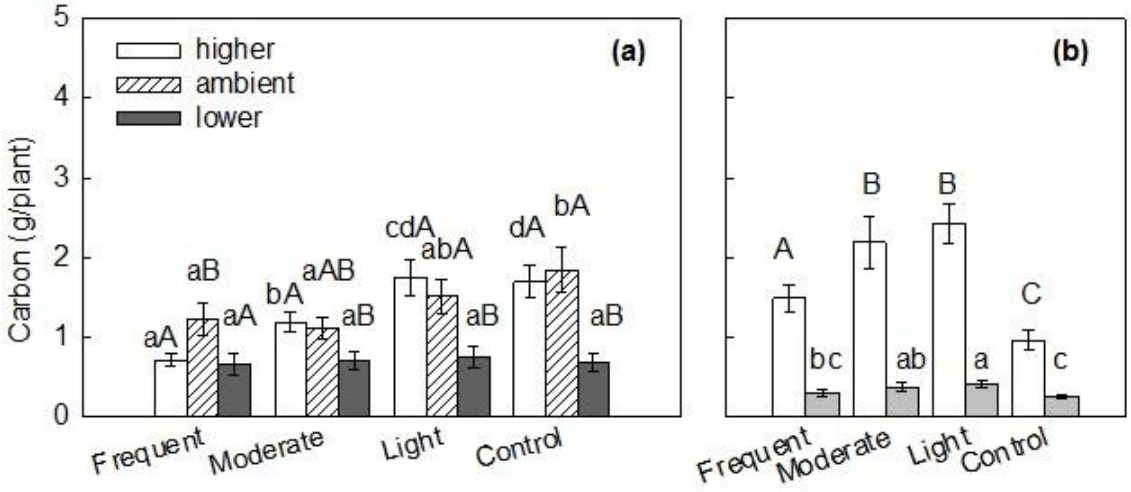

Figure 3.3 (a) Interactive effect of irrigation (higher = 5% above average ambient rainfall, mean = ambient average annual rainfall, lower = 70% of average ambient rainfall) and clipping (frequent = weekly clipped, moderate = biweekly clipped, light = monthly clipped, none = unclipped/control) on belowground C storage of *Chloris gayana* in the pot experiment. Bar graphs with whiskers represent mean (± SE) of belowground C across clipping frequencies and irrigation amounts in the pot experiment. Means in the same irrigation amount followed by the same lowercase letters and means in the same clipping frequency followed by the same uppercase letters are not significantly different by Tukey's HSD test; **(b)** Mean (± SE) above- (white bars) and belowground (gray bars) C of *C. gayana* across clipping frequencies (frequent, moderate, light, and control) in the field plot experiment.

3.3.4: Responses of carbon to changes in irrigation amount

In the pot experiments, decreased irrigation amount significantly reduced agC and bgC in *C. ciliaris* ($F_{(2,61)}$ = 8.49, P = 0.0006 and $F_{(2,61)}$ = 9.55, P = 0.0002, respectively; Fig. 3.4a) as well as agC in *C. gayana* ($F_{(2,61)}$ = 15.03, P < 0.0001; Fig. 3.4b).

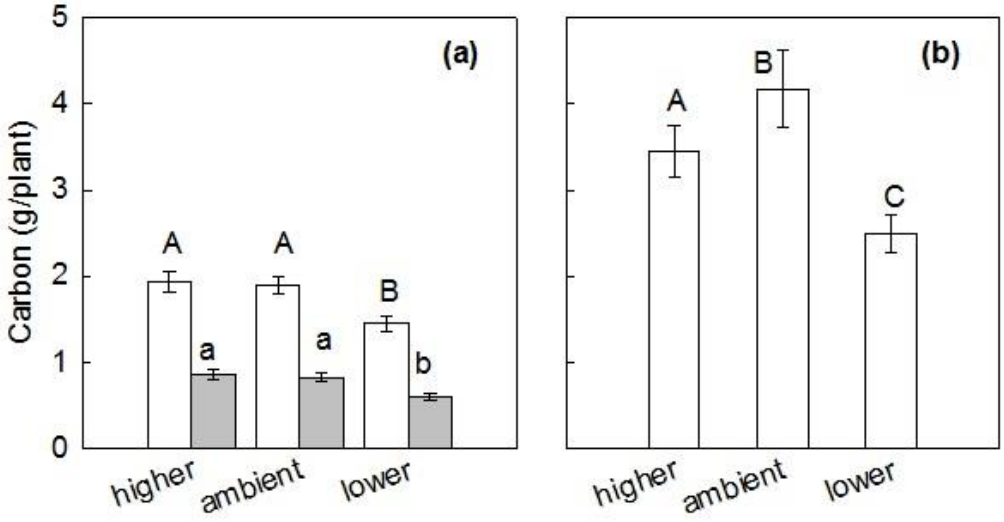

Figure 3.4 (a) Mean (± SE) above- (white bars) and belowground (gray bars) C of *C. ciliaris* across irrigation (higher = 5% above average ambient rainfall, mean = ambient average annual rainfall, lower = 70% of average ambient rainfall), in the pot experiment. **(b)** Mean (± SE) aboveground C of *C. gayana* as affected by irrigation (higher, ambient, lower) in the pot

experiment; we omitted the belowground part because we already presented it in the interactive graph, Fig. 3.3a. Different letters denounce significant difference across treatments by LSD test.

In contrast, in the field plot experiment, there were no observed statistically significant differences among irrigation amounts in both grass species for agC and bgC (data not shown).

3.4: Discussion

3.4.1: Clipping and carbon storage in mature grass tufts

The significantly higher agC in unclipped vs. clipped treatments, also found by Asgharnezhad et al. (2013), indicated that grazing might play a significant role in reducing C storage of mature grasses. The observed low aboveground carbon was caused by the removal of photosynthetic tissues, which was also reported by others (Balogianni et al., 2014). Despite contrasting research findings, there was a general tendency of reduced agC in tropical grasses and higher agC in temperate grasses under grazing (Derner et al., 2006). On the other hand, in our study mature grasses exhibited enhanced bgC storage under clipping and weekly grazing compared to the unclipped control similar to grasses in other field and greenhouse experiments (Veen et al., 2014) as well as under natural cattle grazing (Piñeiro et al., 2010). We found that weekly grazing and clipping had the same effect, suggesting that clipping can stimulate in a similar way how grazing can impact grass C storage (Cuykendall and Marten, 1968). The difference in response to clipping between mature *C. ciliaris* and *C. gayana* might be attributable to their difference in growth habit (rhizomatous and stoloniferous, respectively).

3.4.2: Clipping and carbon storage in newly established grasses

In the field plot and pot experiments, a higher agC under clippings than under non-clipping of freshly grown *C. gayana* and *C. ciliaris* showed that controlled and moderate clipping can enhance C storage of grasses, in contrast to both frequent and no clipping in a newly established pasture. This finding concurred with results from semi-arid grasslands and a greenhouse experiment where significantly higher bgC was found in defoliated compared to non-defoliated grasses (Veen et al., 2014).

We further learned from our study that responses of freshly reseeded grasses to defoliation are more positive than the responses of already established grasses. This might be attributed to young foliage usually exhibiting greater photosynthetic capability than older tissues (Nowak and Caldwell, 1984). Therefore, our finding will greatly contribute to the current young grass management, in restoration endeavors, after reseeding (Mganga et al., 2013; Tebeje et al., 2014) to raise their C storage (Raiesi and Riahi, 2014) besides the primary objective of reseeding

activities, i.e., forage production, which primarily influences the selection of grass species used for restoration purpose (Mganga et al., 2013).

3.4.3: Responses of carbon to changes in irrigation amount

Irrigation was not significant for both grass species in field plot experiments. This might be attributed to horizontal and vertical seepage of water out of the field plots which was not an artifact in the pot experiments. The lower irrigation values that reduced agC and bgC of both grass species in the pot experiments showed that rainfall plays an overriding role in determining C storage of grasses in semi-arid environments. The lower irrigation, a trend similar to the predicted drought scenario for eastern Africa in the face of climate change (Sheffield and Wood, 2008), led to lower C in grass shoots and roots in our study. This result implies that under drought conditions grazing seems less important for C storage of grasses, as was also found by Habtemicael et al. (2014) and Martin et al. (2014). The drought has been known to strongly constrain livestock production in the Borana rangelands (Solomon et al., 2007). Reducing cattle numbers before drought strikes would help grasses to easily recover in the following rainy season and would further prevent losing animals due to starvation.

3.4.4: Combined effects of clipping and irrigation

The significant interactions between clipping and irrigation for bgC suggested that lower grazing pressure can enhance bgC under average or above average rainfall, but not under low rainfall conditions (Oba et al., 2000). Drought-induced morphological, physiological and biochemical changes in plants result from reduced CO_2 assimilation rates due to low stomatal conductance (Anjum et al., 2011). Further, the significantly higher bgC at above average rainfall amounts in the clipped compared to the unclipped *C. gayana* treatment indicated that under controlled grazing a high rainfall amount will play a great role in enhancing the C storage of grasses. This might be an opportunity for east African regions where higher rainfall is predicted under the future climate change scenarios (Christensen et al., 2007).

Therefore, future grazing management should consider resting of grazing areas for better C storage in the belowground parts of grasses, which plays a more relevant role than aboveground biomass in mitigating climate change since more than 90% of organic C in grassland is primarily contributed by roots (Piñeiro et al., 2010). Generally, all OC found in the soil mainly derives from plant debris (Kuzyakov and Domanski, 2000) and plant roots are the primary contributors (Piñeiro et al., 2010). Hence, a change of degraded lands to perennial grassland through restoration activities, such as reseeding and better management afterwards, can greatly contribute to C storage (Tennigkeit and Wilkes, 2008). This implies that grasslands are important C sinks since they can

reduce the unprecedented increase of CO_2 in the atmosphere and thus mitigate climate change effects (Acharya et al., 2012). The rate of rangeland recovery from degradation tends to proportionally increase the grassland productivity, which implies that sound management practices are essential to realizing fewer C losses (Paustian et al., 1997). The strategies for rangelands should focus on managing the degraded areas by reseeding with perennial grasses (Mapfumo et al., 2002), which are suitable for dry environments (Preger et al., 2010; Ruppert et al., 2015). Knowledge of the major drivers of individual-level grass response is important (Zimmermann et al., 2015) because species level response is essential for understanding community level response (Jobbágy and Sala, 2000). Hence, information generated in our research is useful in order to understand responses of grasses to grazing under variable rainfall. Further, the two grass species have global distribution and hence their management would have widespread implications (Boonman, 1993; Marshall et al., 2012). Generally, such local activities have a global impact in the face of climate change in view of the fact that degraded areas are potential for carbon sink due to their worldwide size (Nosetto et al., 2006).

We observed contrasting results in grass C storage between mature and young grasses. Such variation might be attributed to the capability of young foliage to exhibit greater photosynthesis and, thus, greater carbon storage than older tissues. Hence, rangeland management should be based on the age of grasses for better C storage of grasses. Frequent grazing can significantly hamper agC storage in mature *C. ciliaris* and *C. gayana* while light to moderate grazing can stimulate agC and bgC in newly established pastures. Our findings have important implications for the management of grasslands of different ages in areas such as Borana rangelands, where the grass species tested are recommended for restoration of degraded rangelands. Our study showed that the C storage of grasses was overridden by frequent grazing when rainfall was high. Hence, a resting period is recommended for years with increased rainfall for better carbon storage of the study species. Therefore, long-term practiced exclosures and reseeding of degraded areas should be lightly and moderately clipped or grazed to enhance the overall C storage of the rangelands when grasses are young. Such grazing management will improve rangelands as CO_2 sinks and mitigate climate change. Therefore, appropriate grazing management (moderate and light grazing) is needed to foster the capacity of grasses to store more C after reseeding degraded rangelands.

Chapter 4: Modeling Boran cattle populations under climate change and varying carrying capacity*

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*A version of this chapter is published as:

Tuffa, S. and Treydte, A.C., 2017. Modeling Boran cattle populations under climate change and varying carrying capacity. Ecological Modelling, 352, pp.113-127. doi.org/10.1016/j.actao.2017.05.001.

The original publication is available at:

http://www.sciencedirect.com/science/article/pii/S0304380017302077

Abstract

Cattle populations in semiarid rangelands are currently facing severe threats due to erratic rainfall and increasing drought frequencies, leading to poor vegetation quality and a consecutive cattle population decline. However, little is known about how particular sex- and age-cohorts of cattle respond to these environmental threats and on how sales influence population trajectories. In the Borana rangelands, southern Ethiopia, much detailed information is available on the Boran cattle (*Bos indicus*) population demographics, a special breed, which is highly adapted to semiarid environmental conditions. We collected data on Boran cattle demographic and environmental factors such as carrying capacity, market values, and herders´ management decisions. We generated stochastic models and assessed the future development of cattle population trajectories under four different drought scenarios. We analyzed changes in age- and sex-cohorts of cattle populations by introducing different drought frequencies and their effect on vital rates, carrying capacity, and sales. We calibrated the model on the basis of a 12-year data set of a neighboring Boran cattle group. In our population model, the cattle numbers significantly declined after 18 years under the higher drought frequency scenarios (scenarios 3 and 4) while numbers remained high over 100 years for the lower drought frequency scenarios 1 and 2. The sale of senescent and adult females most strongly (77%) affected population trajectories, and model outcomes were most sensitive to sale rates of senescent, adult, and juvenile females compared to vital rates and male sale rates of the population. Management should focus on lowering herd crashes through increasing sale of mature males, which increases feed availability to females during drought years in the Ethiopian Rangelands. Drought early-warning systems and market information must be strengthened so that pre-planned selling of cattle can be realized for a sustainable use of the animal resource.

Keywords: drought scenario; demographic stochasticity; population trajectory; Ethiopia; livestock; rangeland.

4.1: Introduction

4.1.1: The Boran cattle and their habitat

About 58% of sub-Saharan Africa's cattle population is found in eastern Africa, the largest number of which is within Ethiopia, with 56.7 million head of cattle (CSA, 2015; Otte and Chilonda, 2002). Cattle production plays a significant role in Ethiopia's economy, contributing to about 40% of the annual agricultural output and 15% of the gross domestic product (Haile et al., 2011). The Boran cattle, which are grouped under the East African shorthorn cattle known as zebu (*Bos indicus*), inhabit the Borana plateau of southern Ethiopia, semiarid and arid lands of northern and rift valley

provinces of Kenya, and western Somalia and Jubaland of southern Somalia (Rege and Tawah, 1999; Fig. 4.1).

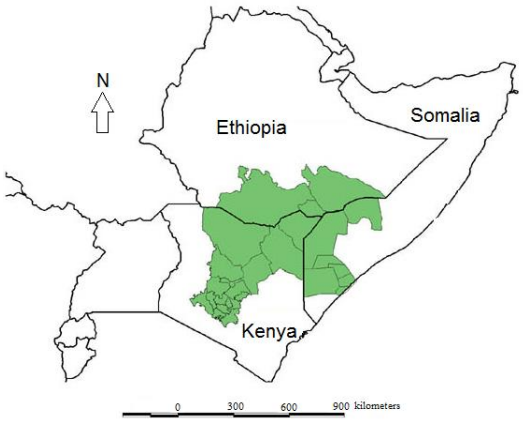

Figure 4.1 Core habitat (green color) of the Boran cattle in east Africa in 2008. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Source:

http://agtr.ilri.cgiar.org/agtrweb/documents/Maps/BreedMaps/boran/boran_dstrb.jpg

Based on the total area of the Borana zone (Riche et al., 2009) and the total livestock population numbers (CSA, 2015), we calculated the latest livestock density of the area at 24.2 TLU (Tropical Livestock Unit) per km^2 (with 16.5 TLU/km^2, 2.7 TLU/km^2, 1.8 TLU/km^2, 1.2 TLU/km^2, and 2 TLU/km^2 of cattle, goat, sheep, donkey, and camel, respectively, based on FAO (1991) TLU conversion factors). This is under the assumption that all areas are accessible for grazing, except settlement areas, which overestimates cattle grazing areas. This livestock density value is similar to the estimated density of 23.5 TLU/km^2 (Homann et al., 2008), but much higher than estimates of 4-16 TLU/km^2 (Coppock, 1994) for the Borana rangelands.

Currently, cattle mortality rates due to drought have reached as much as approximately 70% (Forrest et al., 2014). Little is known about how the Boran cattle population reacts to such drastic dips in population sizes and how this stochasticity would affect population trajectories in the long run. Further, attempts to predict the pastoralists' decisions on selling animals as well as death rates caused by drought occurrence have been rare (Lybbert et al., 2000). Predictive age- and sex-cohorts modeling is of high interest in Borana as it can highlight how mortalities and sales strongly influence the herd development and resilience following drought (Upton, 1989).

4.1.2: Boran cattle adaptation to their environment and their current threat

The Boran cattle are more productive than other local cattle breeds, with quite high rates of reproduction, milk yield, and low mortality rates (Cossins and Upton, 1988a). The Boran cattle are adapted to the arid and semiarid environment of East Africa (Haile et al., 2011), particularly the semiarid Borana rangelands (Homann et al., 2004). Local herders such as Borana pastoralists strongly depend on these animals for their daily livelihoods (Coppock, 1994; Kamara et al., 2005; Zander et al., 2009a; Zander and Drucker, 2008); hence, cattle are the most important livestock species in the Borana pastoral system of Ethiopia and other semiarid regions (Forrest et al., 2014; Kahi et al., 2006; Tolera and Abebe, 2007). Boran cattle strongly contribute to the food security of the rural poor in areas where other agricultural land use systems would not be ecologically sustainable. However, the total dependency on animals has recently come under threat due to recurrent drought and human population pressure (Zander et al., 2009b) as well as increased occupation and privatization of preferred grazing land (Coppock, 1994; Desta and Coppock, 2002). Consequently, Boran cattle have recently undergone drastic population crashes (Angassa and Oba, 2007), which highlights the fragility and the lack of knowledge of their persistence within an increasingly unpredictable environment due to climate change. Further, the Boran breed is under threat from genetic erosion due to the admixture of other breeds that are used for restocking after drought (Alemayehu et al., 2003). To keep the Boran breed as an essential aspect of a sustainable animal production system, Zander et al. (2009b) suggested *in-situ* conservation that must be initiated to maintain the traditional social structures and their livestock. However, little is known about the resilience of Boran cattle and their population dynamics in the face of increasing drought due to climate change (He et al., 2014). Our study wanted to shed light on the population dynamics of this highly threatened but important breed in the Borana rangelands under different drought scenarios.

4.1.3: Carrying capacity of the Borana rangelands

Estimation of carrying capacity is an important requirement for understanding the long-term sustainability of rangelands and the survival probability of the livestock populations inhabiting the area. The potential carrying capacity is usually determined by the availability (quantity and quality) of feed and the stocking rate, which provides the maximum sustainable livestock yield (Eltringham, 1979 cf Fritz & Duncan, 2004). In semiarid rangelands, such as the Borana system, a fixed carrying capacity as predicted in a stable equilibrium model is unlikely (Gillson and Hoffman, 2007) because this does not take the spatial heterogeneity and climate variability of semiarid rangelands into consideration. Hence, equilibrium (density-dependent) models should be

replaced by non-equilibrium (density-independent) models as emphasized by rangeland management today for most semiarid rangelands (Vetter, 2005). The latter employs opportunistic management strategies and mobility rather than estimating a stable carrying capacity. In low-rainfall years, primary productivity is limited and animals will compete for the little forage available (Gillson and Hoffman, 2007). The population cannot persist indefinitely within a certain environment without density dependence occurring (Godfray, 2009). Understanding stochastic population dynamics requires an understanding of the relations between density-dependent (demographic stochasticity) and density-independent (environmental stochasticity) factors.

In semiaid grazing systems, like Borana rangelands, environmental variability has a primary effect on herbivore population dynamics (Illius and O'Connor, 2000). Mobility and resting of pasture had been the main strategy used to manage risk and use the range resources communally and efficiently (Flintan et al., 2011). However, Borana pastoral herd mobility has been weakened (Homann et al., 2004), which has led to rangeland degradation (Nyangito et al., 2008). A recommended stocking strategy under variable rainfall must be urgently provided, which can be achieved by simulation modeling for the current system, assuming no possibility for mobility (Vetter, 2005). In the Borana rangelands when stocking rates are high, the herd is most vulnerable to drought-induced mortality (Desta and Coppock, 2002), which can impose even higher damage to available key plant resource areas (Illius and O'Connor, 1999). The pattern of cattle mortality has closely followed rainfall variability and drought-induced cattle mortality has been caused by pre-drought cattle body condition as a result of feed scarcity (Angassa and Oba, 2007; Starfield, 1990).

In such an unstable system, stochastic models will help to predict scenarios in which rainfall variability could impact population sizes (Otto and Day, 2007). While many population models take carrying capacity into account, which limits population growth (Schärrer et al., 2014), few studies have acknowledged the varying nature of a rangeland´s carrying capacity (Campbell et al., 2006; Walker et al., 1987), depending on environmental factors and increasing herbivore population pressure (Angassa and Beyene, 2003; Halley and Iwasa, 1998). Hence, there is an urgent need to quantify and balance available resources and grazing pressure to minimize drought-induced losses and consecutive rangeland degradation.

4.1.4: The Boran cattle market

The Boran cattle fetch a high price per kg at local markets (Solomon et al., 2003) and have a high export value, particularly in Middle East countries (ILRI, 2008; Farmer, 2010). Such a high sale rate affects the future performance of the herd because herd productivity is expressed as the sum

of all expected sales (Baptist, 1992). Boran pastoralists are not commercial producers but are rather forced to sell animals at a low price due to poor body conditions in drought times (Tiki, 2013). Although drought forces selling of animals due to feed shortages pastoralists hardly sell mature cows during the non-drought years (Pavanello, 2010). It was shown that it is more efficient if pastoralists plan marketing of male animals before a drought occurs so that feed availability to the cows, which play a major role in herd growth (ILCA, 1985), will be guaranteed and a rush to sell animals during drought periods is prevented (Pavanello, 2010; Tiki, 2013).

4.1.5: The importance of population growth models

Population growth models are useful planning tools for predicting future population structures and off-takes under different policy options (Upton, 1989). Particularly, for livestock production systems, models can support current and design future management decisions (Hastings, 1997, Martin et al., 2014; Upton, 1986). Finding the appropriate level of model complexity is one of the hardest problems in applying models to managing biological resources (Getz, 1988). Further, the actual herd-growth process in semiarid areas is highly variable and is, therefore, difficult to accurately predict (Upton, 1989). Models require detailed studies to analyze how population sizes are influenced by the random recurrence of drought. In our herd growth model, we captured this variability by introducing random disturbance as a result of drought events. We used a stochastic model based on Berkeley Madonna (Macey et al., 2009) to understand the influence of environmental and demographic stochasticity on a structured cattle population in the Borana rangelands, southern Ethiopia.

Most population models assume that individuals in a population have equal demographic characteristics (Lesnoff et al., 2012; Shabb et al., 2013) while many natural populations comprise individuals with different vital parameters that differently respond to environmental factors such as drought. So far, no model has been developed considering drought as a random factor influencing the trajectories of this cattle breed over a continuous time scale. The objectives of this study, therefore, were to (i) model Boran cattle population dynamics based on three major factors, namely environmental constraints (i.e., varying carrying capacity), cattle population demography, and sales, (ii) identify parameters that most strongly influence the population trajectory, based on sensitivity analyses, and (iii) identify animal classes (age- and sex-cohorts), which should be targeted during shocks to ensure long-term and sustainable productivity.

4.2: Methodology

4.2.1: Study area

We used parameters that were generated from Borana rangelands, which occupy an area of about 95,000 km^2 in southern Ethiopia (Desta and Coppock, 2004) and are characterized by a semiarid to arid climate (Haile et al., 2011; Kamara et al., 2005). Despite high ecological potential in relation to livestock production, the rangelands are under increasing pressure (Kamara et al., 2005).

4.2.2: Climatic conditions

The rainfall of the Borana rangelands follows a bimodal pattern, with a mean annual rainfall (± SD) at our research area of 645 (± 232) mm, ranging from 327 to 1343 mm (Yabello Research Centre Weather station and National Meteorological Agency, Personal comm.). The mean monthly temperature is 20°C, with average maximum and minimum temperatures of 26°C and 14°C, respectively (Fig. 4.2).

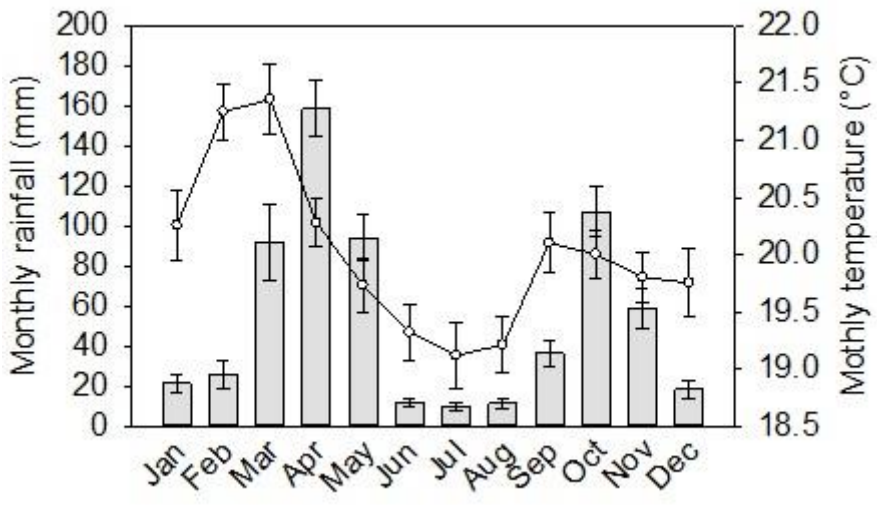

Figure 4.2 Mean (± SE) monthly precipitation (bar graph) and temperature (line graph) from 1984 to 2013 in Yabello district, Borana (Yabello Research Centre Weather Station and National Meteorological Agency).

Cattle population numbers followed the rainfall patterns in the Borana rangelands, indicating a peak in numbers when annual rainfall was highest (1343 mm) and being low at low annual rainfall (874 mm) (Fig. 4.3). This wide range in annual rainfall dictates high fluctuation in animal numbers. We collected observed population data from annual reports of the Central Statistical Agency (CSA) for the years 2004 until 2015, together with associated rainfall data (Fig. 4.3).

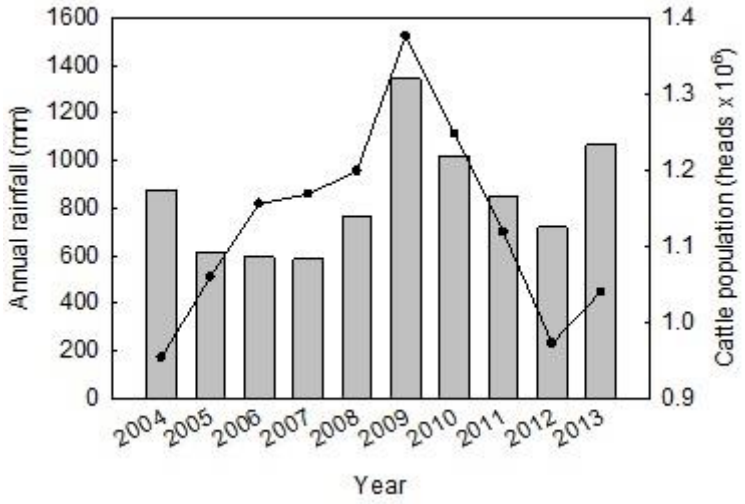

Figure 4.3 Annual rainfall (gray bars) and observed cattle population (black line) in the Borana zone, southern Ethiopia.

Source:

Yabello Research Centre Weather Station and National Meteorological Agency, and CSA for 2004 - 2013 annual reports.

4.2.3: Population dynamics

The age- and sex-cohorts approach has been applied in modeling different animal population trajectories (Charlesworth, 1994; Coulson et al., 2008; Treydte et al., 2011; Upton, 1986) and can be very helpful in predicting population trajectories over time. In Boran cattle populations, it has been reported that drought does not affect different age- and sex-cohorts uniformly, where birth and mortality are a function of age and sex (Coppock, 1994). External factors (environmental stochasticity and market pressure) have a strong effect on cattle breeding in east Africa (Zander, 2011). Boran cattle production highly depends on the natural resources, which are greatly disturbed by recurrent drought. While natural pastures are the main feed source for Boran cattle pasture productivity has recently declined and resulted in high livestock mortality (Catley et al., 2014). Different age and sex groups of Boran cattle are known to be differently predisposed to drought intensity, with infants being most strongly affected (Table 1).

Table 1. Parameters used to model the population dynamics under drought scenarios.

Label	Description	Unit	Non-drought year	Drought year	Optimized parameter value	*D*	References
K	Potential carrying capacity	TLU/km^2	16[a]; 23.5[b]	4[a]; 11.8[b]	64	0.71	(Coppock, 1994[a]; Cossins and Upton, 1988[ab]; Homann et al., 2008[b])
b_m	Birth rate from mature cows	%	75[a]; 53-75[b]; 55[c]	9[d]	75	0.71	(Angassa and Oba, 2007[c]; Mulugeta Asefa, 1990[b]; Coppock, 1994[d]; Cossins and Upton, 1988[ab], 1987[a])

b_y	Birth rate from young cows	%	28	9	28	0.71	(Coppock, 1994)
d_i	Infant death rate (< 1yr)	%	18[a]; 22-25[b]; 18-25[c]	90[d]; 70-90[c]	18	0.9	(Coppock, 1994[c]; Cossins and Upton, 1988[d], 1987[b]; Holden et al., 1991[a])
d_{mc}	Male calves death rate (1-2yrs)	%	13[b]	57[a]	13	0.7	(Coppock, 1994[a]; Nicholson & Cossins, 1984[b] as cited in Cossins and Upton, 1987)
d_{mj}	Juvenile male death rate (2-3yrs)	%	5[a]	8-10[b]	5	0.6	(Mulugeta Asefa, 1990[b] as cited in Coppock, 1994; Nicholson & Cossins, 1984[a] as cited in Cossins and Upton, 1987)
d_{ma}	Adult male death rate (3-4 yrs)	%	2[a]	22[b]	2	0.4	(Coppock, 1994[b]; Nicholson & Cossins, 1984[a] as cited in Cossins and Upton, 1987)
d_{ms}	Senescent male death rate (4-10 yrs)	%	3	22	2	0.22	(Coppock, 1994)
d_{fc}	Female calves death rate (1-2 yrs)	%	13[b]	57[a]	13	0.7	(Coppock, 1994[a]; Nicholson & Cossins, 1984[b] as cited in Cossins and Upton, 1987)
d_{fj}	Juvenile female death rate (2-3yrs)	%	5[a]	8-10[b]	5	0.6	(Mulugeta Asefa, 1990[b] as cited in Coppock, 1994; Nicholson & Cossins, 1984[a] as cited in Cossins and Upton, 1987)
d_{fa}	Adult female death rate (3-4 yrs)	%	2[a]	10[b]	2	0.4	(Coppock, 1994[b]; Nicholson & Cossins, 1984[a] as cited in Cossins and Upton, 1987)
d_{fs}	Senescent female death rate (4-10 yrs)	%	3	45	2	0.45	(Coppock, 1994)
s_{mj}	Juvenile male sale rate	%	4-8	10	17	0.19	(Coppock, 1994)
s_{ma}	Adult male sale rate	%	26[a];9[b]	35	17	0.2	(Coppock, 1994[a]; Negassa and Jabbar, 2008[b])
s_{ms}	Senescent male sale rate	%	26[a];9[b]	35	18	0.35	(Coppock, 1994[a]; Negassa and Jabbar, 2008[b])
s_{fj}	Juvenile female sale rate	%	3	5	3	0.03	(Coppock, 1994)
s_{fa}	Adult female sale rate	%	4-5	5	3	0.05	(Coppock, 1994)
s_{fs}	Senescent female sale rate	%	4-5	5	3	0.05	(Coppock, 1994)
sl	Slaughter rate	%	4		4		(Coppock, 1994)
r	Sex ratio	%	50		50		(Ezanno, 2005)

Birth rates differ based on maturity of cows (Coppock, 1994), which was captured in our structured population modeling, assuming a 50:50 sex ratio (Ezanno, 2005). Further, we assumed that death rates and sale rates proportionally increased in all age- and sex- cohorts when drought occurs (Table 1; Fig 4.4).

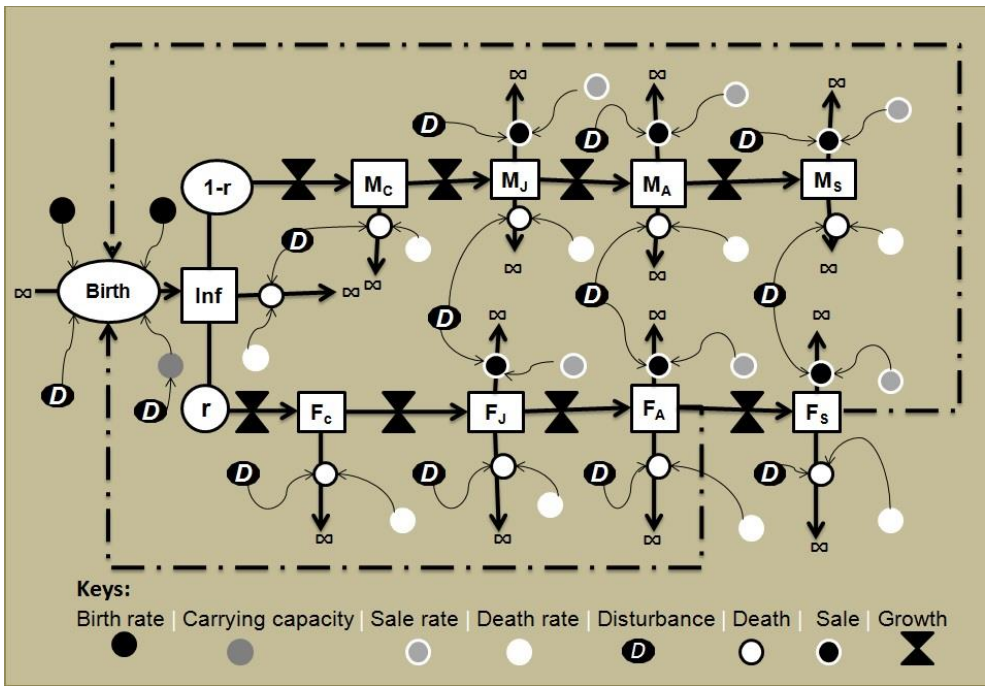

Figure 4.4 Schematic illustration of Boran cattle (*B. indicus*) population dynamics in the Borana rangelands. This herd-growth model illustrates how the drought and animal offtake, together with the numbers of animals in each sex- and age-cohorts in the following year is determined by the numbers of animals in each cohort in the current year and their rates of production and survival under influence of random occurrence of drought (D). We omitted from this flow chart the slaughtering rate to minimize the number of connections in the model for simplification. The following age- and sex-cohorts are distinguished: F_C = female calves, F_J = female juvenile, F_A = adult female, F_S = senescent female, M_C = male calves, M_J = male juvenile, M_A = adult male, and M_S = senescent male, as well as the infants (inf); each process of growth from one age-cohort to the next corresponds to growth of female infants, growth of female calves, growth of female juvenile, female adult growing old; growth of male infants, growth of male calves, growth of male juvenile, and male adult growing old; r = sex ratio; Death = death of respective age-cohort; Sale = sale of respective age-cohort.

4.2.4: Vital rates

For our model, we used parameter values on vital rates (birth rates, death rates) and age at first calving from literature sources generated from the Borana rangelands (Table 1) and cattle numbers from the Borana zone's annual statistical reports (CSA, 2015, 2014, 2013, 2012, 2011, 2010, 2009, 2008, 2007, 2006, 2005, 2004). We assumed that most Boran cattle start calving at the age of 4 years (Table 1 and literature cited therein). Death rates vary by age- and sex-cohorts in non-drought and drought years (Table 1).

4.2.5: Drought as environmental disturbance

In the context of this paper, drought refers to agricultural drought that leads to cattle mortality as a result of loss in rangeland productivity (Boken, 2005; Oba, 2001) because meteorological drought does not necessarily reflect causes of livestock mortality (Angassa and Oba, 2007; see

also Fig. 4.3). There should be at least two consecutive meteorological droughts for agricultural drought to happen in the Borana rangelands (Coppock, 1994). Therefore, in our model, we randomly injected the disturbance at different frequencies in a continuous time scale, i.e., as a pulse in Berkeley Madonna, based on mean of drought frequency as random factors with standard deviation. This pulse increases or decreases population size (during non-drought and drought years, respectively), occurring randomly, initiated on a fixed time (5 years) when the first drought hits the population (Macey et al., 2009). Drought affected population trajectories through various model parameters (Table 2, equations 1.10, 1.19 - 1.27, and 1.29 - 1.34; Fig. 4.4) as such selling events. We introduced each drought scenario separately as a normally distributed random factor with mean μ and standard deviation SD, N(μ, SD), to the model in continuous time scale as a pulse in Berkeley Madonna packages (Macey et al., 2009; Table 2, Equations 1.36-1.53) in such a way that it creates boom-and-bust to population size (Desta and Coppock, 2002). The mean and standard deviation, (μ,SD), of drought scenarios 1, 2, 3, and 4 were (20,15), (15,11.25), (10,7.50), and (5,3.75), respectively. In each run, the first disturbance occurred at year 5 under all scenarios so that results from each scenario run were comparable and hence 99 out of 100 runs had drought occurring at a random interval (Macey et al., 2009) per each scenario. The disturbance to carrying capacity was introduced as *D_K = pulse(K*D,5,Random_factor)* where *K*D* is the volume reduced during drought events with an optimized value (calibrated value) of carrying capacity (*K*) and disturbance (*D*) in Table 1; 5 is the first pulse at year 5; and *Random_factor* is the repeated interval or drought frequency (Table 2, Equation 1.53). We ran our model under various scenarios, altering the frequency of drought occurrence (Coppock, 1994; Homann et al., 2003; Solomon et al., 2007).

In semiarid environments, drought is a common cause of herbivore mortality (Ellis and Swift, 1988). Our drought frequencies were based on the assumption that drought frequencies will increase in the future due to climate change according to the trend for Ethiopia's agricultural drought years from 1965 to 2013 (Masih et al., 2014; Fig. 4.5).

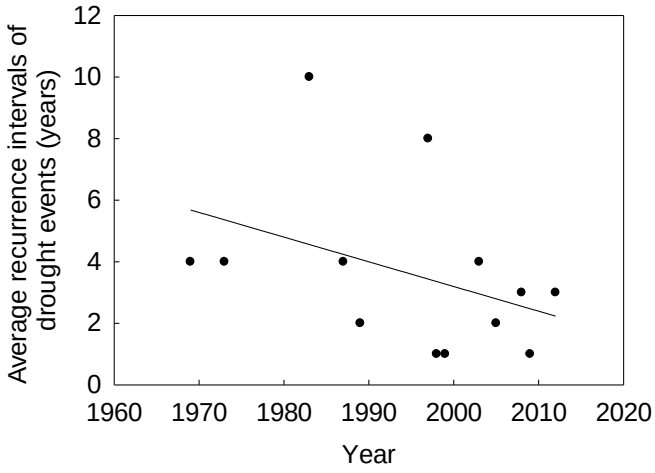

Figure 4.5 The year intervals between recurrent drought events. Filled circles indicate the number of non-drought years between consecutive drought years based on 1965-2012 rainfall data.

Disturbance analyses, which explore the effects of changes in the vital rates of population growth, have become a standard part of demographic practices to account for possible disturbance (Horvitz et al., 1997). Given the vital and sale rates, the future herd structure and production levels can be predicted in areas with rather uniform climate conditions using a herd growth model (Upton, 1989). In the Borana arid and semiarid ecosystem, drought plays a major role (ILCA, 1992), and hence, we included a disturbance "drought" to our herd growth model as a major element governing population size. A drought was recorded to happen once every twenty years in Borana (Cossins and Upton, 1988b). However, recent reports showed that it can happen once every three to seven years (Coppock, 1994; Desta and Coppock, 2002; Homann, 2004). In our model, we used drought recurrence as a random factor within a duration of 20 years as an average drought interval for the area, and then increased this average frequency by 5 year intervals to come up with four drought scenarios (scenarios 1, 2, 3, and 4, i.e., once every 20, 15, 10, and 5 years, respectively).

4.2.6: Model description

We developed a stochastic model of population dynamics of Boran cattle (Fig. 4.4). We assumed that the cattle population was genetically homogeneous, i.e., individuals can be legitimately classified solely by sex and age. Additionally, we assumed that the population is homogeneously distributed over the Borana plateau due to broad-scale foraging behavior and long range cattle dispersal, exerting uniform grazing pressure on the patchy resources, which allowed the modeling only in a temporal rather than a spatial context. However, we captured the environmental stochasticity through a varying carrying capacity (Jeppsson, 2009) that is caused by drought recurrence. Further, we assumed that there is a continuous growth of some members within each group from lower age-group to the next level at any instantaneous time of the year (Engen et al.,

2007). Hence, to accommodate this reality, we assumed that the Boran cattle population growth was continuous. Matrix models project discrete population stages over discrete time steps (Caswell et al., 1997; Horvitz et al., 1997) and usually focus on female segments of the population (Sæther et al., 2013). We used a logistic model with added environmental stochasticity (Di Fonzo et al., 2013) in differential equations (Rockwood, 2015; Table 2, Equation 1.1 - 1.9), which included continuous growth during a non-drought year and continuous declines during a drought year. We used the Runge-Kutta method in the order of four built-in integration of Berkeley Madonna (version 8.3.18) to numerically solve our ordinary differential equations at an annual integration time step for the population growth interval (de Roos, 1997; Macey et al., 2009; Appendix A Fig. 1). We preferred Berkeley Madonna as a dynamic system software package because it has a higher computational power than Stella software (Rizzo et al., 2006) and runs more quickly, has added unique features, is self-contained, and a user friendly modeling tool (Macey et al., 2009). We used a logistic growth model by including the per capita growth rate as well as a varying carrying capacity between non-drought and drought year values. We omitted infants from the total population in our carrying capacity calculations because we assumed that they do not compete for available feed (Table 2, Equation 1.10).

Table 2. Equations used in cattle population modeling as referred to in the text.

Equation numbers (**No.**) are given for reference in the text. Total cattle population (*Total_pop*) is the sum of different sex- and age-cohort categories (Eq. 1.35).

Parameter	***Sex***	***Age class***	***Differential equation***	***Equation No.***
	Both	Infant	$\frac{\partial I}{\partial t} = birth - death_I - G_{FI} - G_{MI}$	1.1
	Female	Calf	$\frac{\partial FC}{\partial t} = G_{FI} - G_{FC} - death_{FC}$	1.2
		Juvenile	$\frac{\partial FJ}{\partial t} = G_{FC} - G_{FJ} - death_{FJ} - sale_{FJ}$	1.3
		Adult	$\frac{\partial FA}{\partial t} = G_{FJ} - G_{FA} - death_{FA} - sale_{FA}$	1.4
		Senescent	$\frac{\partial FS}{\partial t} = G_{FA} - sale_{FS} - death_{FS}$	1.5
	Male	Calf	$\frac{\partial MC}{\partial t} = G_{MI} - G_{MC} - death_{MC}$	1.6
		Juvenile	$\frac{\partial MJ}{\partial t} = G_{MC} - G_{MJ} - sale_{MJ} - death_{MJ}$	1.7
		Adult	$\frac{\partial MA}{\partial t} = G_{MJ} - G_{MA} - sale_{MA} - death_{MA}$	1.8
		Senescent	$\frac{\partial MS}{\partial t} = G_{MA} - death_{MS} - sale_{MS}$	1.9
Parameter	***Sex***	***Age class***	***Input and output population flows***	***No.***
Birth	Both	Infant	$birth = ((FS*(b_m - D\_b_m)) + (FA*(b_y - D\_b_y))) *(1-(Total\_Pop - I)/(K - D\_K))$	1.10
Growth	Female	Infant	$G_{FI} = (I - death_I)*r$	1.11
		Calf	$G_{FC} = FC - death_{FC}$	1.12
		Juvenile	$G_{FJ} = FJ - death_{FJ} - sale_{FJ}$	1.13

		Adult	$G_{FA} = FA - death_{FA} - sale_{FA}$	1.14
Growth	Male	Infant	$G_{MI} = (I - death_I) * (1 - r)$	1.15
		Calf	$G_{MC} = MC - death_{MC}$	1.16
		Juvenile	$G_{MJ} = MJ - death_{MJ} - sale_{MJ}$	1.17
		Adult	$G_{MA} = MA - sale_{MA} - death_{MA}$	1.18
Death	Both	Infant	$death_I = d_I * I + D\_I$	1.19
	Female	Calf	$death_{FC} = d_{fc} * FC + D\_d_{fc}$	1.20
		Juvenile	$death_{FJ} = d_{fj} * (FJ - sale_{fj}) + D\_d_{fj}$	1.21
		Adult	$death_{FA} = d_{fa} * (FA - sale_{FA}) + D\_d_{fa}$	1.22
		Senescent	$death_{FS} = d_{fs} * (FS - sale_{FS}) + D\_d_{fs}$	1.23
Death	Male	Calf	$death_{MC} = d_{mc} * MC + D\_d_{mc}$	1.24
		Juvenile	$death_{MJ} = d_{mj} * (MJ - sale_{MJ}) + D\_d_{mj}$	1.25
		Adult	$death_{MA} = d_{ma} * (MA - sale_{MA}) + D\_d_{ma}$	1.26
		Senescent	$death_{MS} = d_{ms} * (MS - sale_{MS}) + D\_d_{ms}$	1.27
Slaughtering	Total pop		$slaughter = sl * (Total\_Pop - I)$	1.28
Sale	female	Juvenile	$sale_{FJ} = FJ * s_{fj} + D\_s_{fj}$	1.29
		Adult	$sale_{FA} = FA * s_{fa} + D\_s_{fa}$	1.30
		Senescent	$sale_{FS} = FS * s_{fs} + D\_s_{fs}$	1.31
Sale	male	Juvenile	$sale_{MJ} = MJ * s_{mj} + D\_s_{mj}$	1.32
		Adult	$sale_{MA} = MA * s_{ma} + D\_s_{ma}$	1.33
		Senescent	$sale_{MS} = MS * s_{ms} + D\_s_{ms}$	1.34
Total population		Total_pop	$Total\_Pop = (I + FC + FJ + FA + FS + MC + MJ + MA + MS) - sl * (FC + FJ + FA + FS + MC + MJ + MA + MS)$	1.35
			Introduction of disturbance as a random factor	
d_I		Infant	$D\_d_I = pulse(I * D, 5, Random\_factor)$	1.36
d_{fc}	Female	Calf	$D\_d_{fc} = pulse(FC * D, 5, Random\_factor)$	1.37
d_{fj}		Juvenile	$D\_d_{fj} = pulse(FJ * D, 5, Random\_factor)$	1.38
d_{fa}		Adult	$D\_d_{fa} = pulse(FA * D, 5, Random\_factor)$	1.39
d_{fs}		Senescent	$D\_d_{fs} = pulse(FS * D, 5, Random\_factor)$	1.40
d_{mc}	Male	Calf	$D\_d_{mc} = pulse(MC * D, 5, Random\_factor)$	1.41
d_{mj}		Juvenile	$D\_d_{mj} = pulse(MJ * D, 5, Random\_factor)$	1.42
d_{ma}		Adult	$D\_d_{ma} = pulse(MA * D, 5, Random\_factor)$	1.43
d_{ms}		Senescent	$D\_d_{ms} = pulse(MS * D, 5, Random\_factor)$	1.44
s_{fj}	Female	Juvenile	$D\_s_{fj} = pulse(FJ * D, 5, Random\_factor)$	1.45
s_{fa}		Adult	$D\_s_{fa} = pulse(FA * D, 5, Random\_factor)$	1.46
s_{fs}		Senescent	$D\_s_{fs} = pulse(FS * D, 5, Random\_factor)$	1.47
s_{mj}	Male	Juvenile	$D\_s_{mj} = pulse(MJ * D, 5, Random\_factor)$	1.48
s_{ma}		Adult	$D\_s_{ma} = pulse(MA * D, 5, Random\_factor)$	1.49
s_{ms}		Senescent	$D\_s_{ms} = pulse(MS * D, 5, Random\_factor)$	1.50

b_y	From young cow	$D\_b_y = pulse(b_y * D, 5, Random\_factor)$	1.51
b_m	From mature cow	$D\_b_m = pulse(b_m * D, 5, Random\_factor)$	1.52
K	Carrying capacity	$D\_K = pulse(K * D, 5, Random\_factor)$	1.53

The input variables included age-specific birth rates, age- and sex-specific death rates, and sale rates. We assumed slaughter rates apply for the entire population excluding calves (Table 2, Equation 1.28). The temporal changes of each stock are formulated as a set of nine Ordinary Differential Equations (Table 2, equations 1.1 to 1.9) in a continuous version of the logistic model (Butcher, 2008; Gonze, 2015; Macey et al., 2009). While the carrying capacity is usually kept constant in other population models (Lesnoff et al., 2012; Shabb et al., 2013) each input variable and the carrying capacity continuously varied between non-drought and drought year values in our model. This allowed our model to behave in both a density-dependent and density-independent way at times, which is a realistic condition in a semiarid environment with a varying carrying capacity (Sasaki, 2010; Vetter, 2005). In our model assumptions, the carrying capacity of the Borana rangeland declined in drought years and bounced back to its previous value in non-drought years. Further, our carrying capacity also reduced over time after subsequent droughts had occurred, resulting in consecutively declining cattle populations.

We calculated the carrying capacity as head of cattle for the present Borana zone rangeland area (Riche et al., 2009) minus the average area occupied by settlement (Gurmessa et al., 2013; Haile et al., 2010). In our model, the varying carrying capacity (*K*) changed with the primary production responses following rainfall patterns (Nyangito et al., 2008), thereby including environmental stochasticity to our population modeling (Jeppsson, 2009). We calibrated *K* in a good year (i.e., optimized parameter value), and then reduced by a random disturbance factor (*D*) at every drought event (Table 1).

In our model, we included effects of drought as a random disturbance, *D*, which decreases the herd size at each event of the given scenarios. The *D* value was based on a percentage change from the calibrated values of non-drought and drought years in the population size (Table 1). This factor randomly impacted demographic (vital rates) and environmental (carrying capacity and sale rates) parameters , i.e., increased deaths and sales and decreased birth of the population as well as the carrying capacity (Table 2, equations 1.10, 1.19 - 1.27 and 1.29 - 1.34) during drought years only. Sale rates of the Boran cattle differed across age and sex of individuals (Coppock, 1994; Cossins and Upton, 1988b; Table 1). In our model, selling rates were dependent on age and sex that co-varies with a drought event (Coppock, 1994). Like other parameters in our model, sale rates had two values, one for a non-drought year and another for a drought year (Table 1). We took optimized values after calibration (Table 1) based on literatures values for drought or non-drought years

(Table 1). Effects of drought on each parameter, i.e., potential carrying capacity, birth rates, death rates, and sale rates, differed with varying age- and sex-cohorts. The slaughtering rate remained constant as demands to slaughter an animal were supposed to be the same, irrespective of a drought year.

We separately ran the model 100 times for each scenario and computed average population trajectories over 100 years. Further, taking two extreme scenarios, scenarios 1 and 4, we projected the population to see how changes in the sale of male and death of infants change the entire population size (Fig. 4.11). Therefore, in our model, we saw how increased harvesting of males in combination with reduced calf mortality influenced the population trajectories under different drought scenarios.

4.2.7: Model calibration and validation

For model calibration, we used a 12-year (2004 to 2015) data set of a neighboring Boran cattle herd (CSA, 2004 – 2015) and compared it with the average model trajectory for the same time span based on 100 model runs (Rykiel, 1996; Fig. 4.6). We ran the model in Monte Carlo simulation using the average feature of 100 times batch runs (Goel and Dyn, 1974; Macey et al., 2009; Treydte et al., 2011). The algorithm we used in the calibration of Berkeley Madonna represents a curve fit. To do this, we used the "multiple fit" function in the "curve fit" dialogue and added a 12-year dataset to the fits. Each 12-year dataset pair of simulated vs. observed had a relative weight, which allowed us to control the importance of each pair. Berkeley Madonna multiplied the deviation of each pair by its weight, and then summed these products to compute the overall deviation to be minimized (Doherty, 2004; Macey et al., 2009). For the drought scenarios, we used optimized parameter values (Table 1) with the best fit for observed and simulated population sizes. The calibrated parameter values created in this way fell within the range of parameters indicated in literature (Table 1).

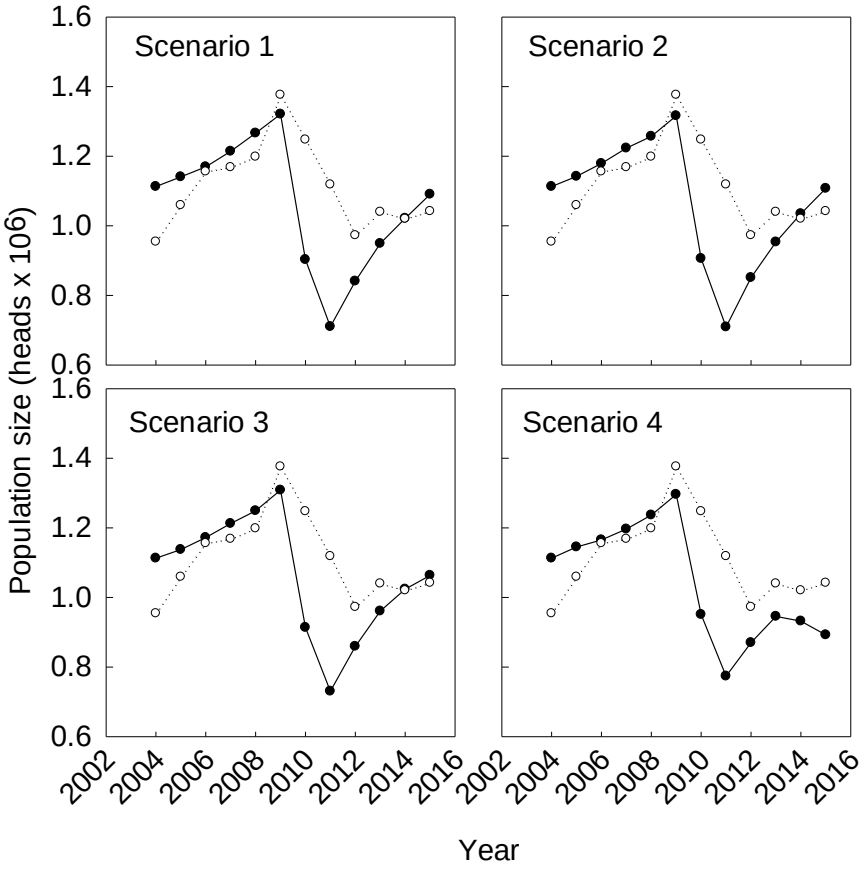

Figure 4.6 Simulated and observed numbers of cattle under four different scenarios (1, 2, 3, and 4) over the first 12 years of model simulation. The solid line represents the optimal fit through calibration of the simulated population trajectory based on 100 runs. The dashed line represents the real population (observed). Scenario 1 = drought frequency happening randomly once every 20 years; Scenario 2 = drought frequency happening randomly once every 15 years; Scenario 3 = drought frequency happening randomly once every 10 years; Scenario 4 = drought frequency happening randomly once every 5 years.

We used the primary validation techniques, i.e., internal and face validities, (Sargent, 2013), the former being particularly applicable to stochastic models (Rykiel, 1996). The increasing and decreasing patterns in both observed and predicted population sizes (Fig. 4.6) are in line with this validity technique. The internal validity of the models in all scenarios showed a high amount of consistency as indicated by R^2 values of 0.86, 0.94, 0.79, and 0.99 for scenarios 1, 2, 3, and 4, respectively (Fig. 4.7), indicating high repeatability of the model after multiple runs.

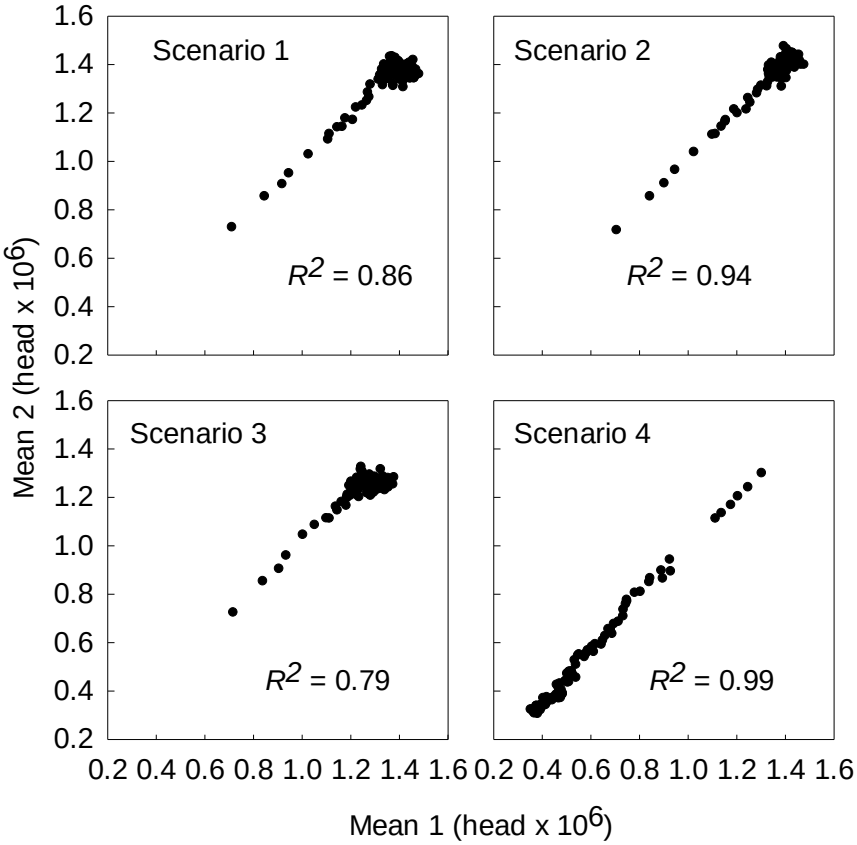

Figure 4.7 Mean internal validity values as indicator of model repeatability. Means 1 and 2 were obtained by the Monte Carlo method after running the model 100 times under each scenario.

4.2.8: Sensitivity analyses

In the sensitivity analyses, we determined the vital rate values used in our model with variations representing each parameter uncertainty from an extensive literature review (Angassa and Oba, 2007; Coppock, 1994; Cossins and Upton, 1988, 1987; Ezanno, 2005; Holden et al., 1991; Table 1). Sensitivity analyses were performed internally as relative parameter sensitivity with Berkeley Madonna (Macey et al., 2009), which computes sensitivity, $S_{(t)}$, of a variable V to a parameter P as

$$S_{(t)} = \left(V_{2(t)} - V_{1(t)}\right) \Big/ \Delta$$

Where, $V_{1(t)}$ and $V_{2(t)}$ are results of the 1st and 2nd run of the model with all parameters at their specified values; and Δ is the amount, 0.001 x P, that is added to adjust parameter P.

We also ran the model to see its sensitivity to changes in the senescent male sale rate individually after altering its value by +20%, +10%, -10%, and -20%. We further repeated the analysis by combining a doubled value of senescent male sale rate and a halved value of infant mortality to see the population dynamics under an altered management, which includes higher male sale rates and provision of supplemental feeding of calves.

4.3: Results

4.3.1: Boran cattle population trajectories

Predicted cattle population trajectories varied around the mean as dictated by random drought events, which influenced the modeling parameters and, consecutively, population growth. In scenario 1, the predicted population trajectories showed a steep increase in the first year, followed by a drastic decline after year 5 of the simulation, i.e., the drought year. Subsequently, a slow recovery took place around 1.39 (± 22%) mio head of cattle in the long run (Fig. 4.8).

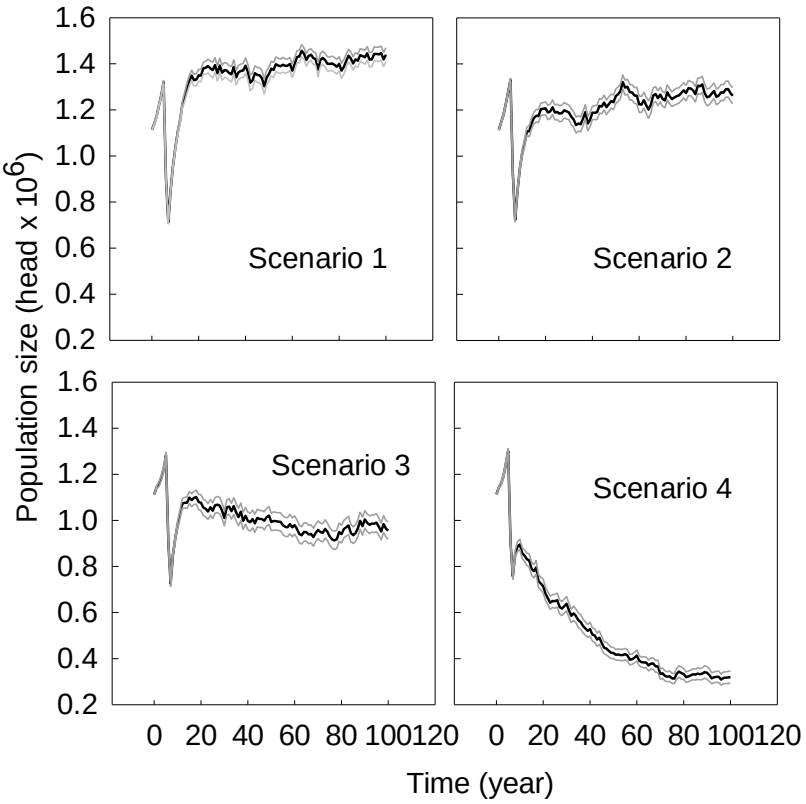

Figure 4.8 Mean cattle population trajectories, which were generated through 100 times model runs under four scenarios (scenario 1 = once every 20 years, scenario 2 = once every 15 years, scenario 3 = once every 10 years, and scenario 4 = once every 5 years) with an initial population size of 1.11 mio that were subjected to random disturbance. The black and gray lines represent the means and 95% confidence intervals, respectively, of the population sizes after 100 model runs. Overall population declines with increasing drought frequency.

In scenario 2, the population size leveled off at 1.24 (± 27%) mio head of cattle (Fig. 4.8). In scenario 3, the population size leveled off and fluctuated around 0.99 (± 38%) mio head of cattle in the long run, which was slightly lower than that of scenarios 1 and 2 (Fig. 4.8). In scenario 4, the population size dropped below 0.43 (± 60%) mio head of cattle (Fig. 4.8). In scenario 4, particularly from year 5 to 65 the decline in population size was rather rapid (Fig. 4.8) and the stochastic growth rate fluctuated highly (Appendix A Fig. 2), which showed more diverse population size out comes under scenario 4 compared to the other scenarios.

4.3.2: Sensitivity analysis

Cattle population trajectories under different scenarios were sensitive to all model parameters (Appendix B Fig. 1). The relative sensitivity levels were indicated by the negative or positive numbers being removed from or added to the population, respectively. The sale of females, relative to other parameters, severely reduced the population growth in the long run in scenario 4. Generally, population trajectories were most sensitive to senescent female sale rate (s_{fs}), followed by juvenile female sale rate (s_{jf}) in scenario 4. Comparing all parameters, the population trajectories under all scenarios were most strongly influenced by the sale of female animals. In scenarios 1, 2, 3, and 4, the sale of female cattle relative to other model parameters reduced the population size by 97%, 98%, 95%, and 95%, respectively (Fig. 4.9) over 100 years. In contrast, the model was least sensitive to female calf death rate (d_{fc}), juvenile female death rate (d_{fj}), birth rates (b_m, b_y), juvenile male sale rate (s_{mj}), adult male sale rate (s_{ma}), senescent male sale rate (s_{ms}), and infant death rate (d_i) (see Appendix B Fig. 1).

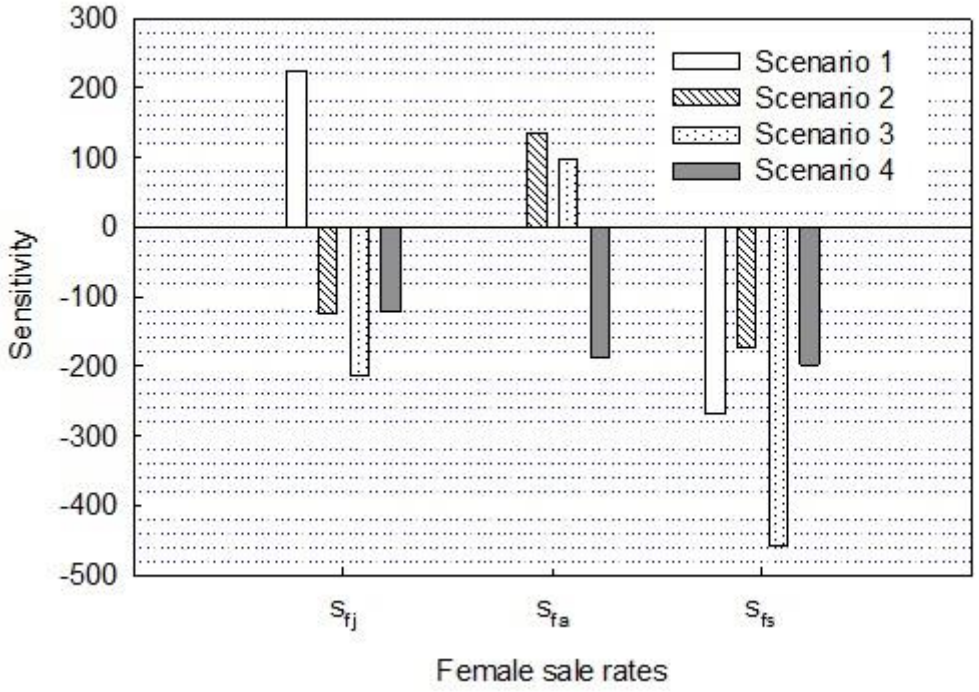

Figure 4.9 Relative sensitivity of population sizes to female sale rates: S_{fj} = sale rate of juvenile females, S_{fa} = sale rate of adult females, and S_{fs} = sale rate of senescent females. The model reacted to these female sale-related parameters most strongly – the weaker responses to other parameters are shown in Appendix B Fig. 1.

When we removed the sale rate of females and compared all other model parameters, our model strongly reacted to death rate of senescent males (Appendix B Fig. 2). When we altered the sale rate of senescent males by +20%, +10%, -10%, and -20% all population trajectories under scenario 4 strongly declined (Fig 4.10).

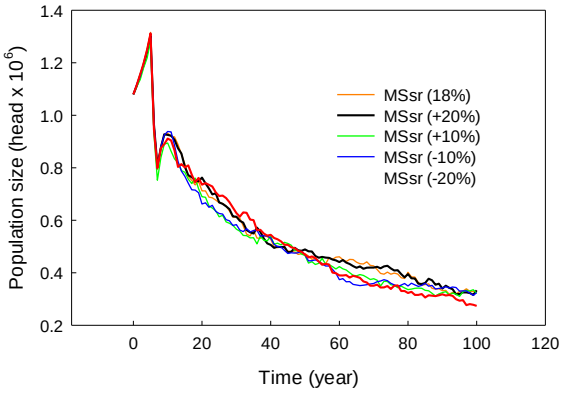

Figure 4.10 Cattle population sensitivity to altered sale rates from the initial value (18%) of senescent males by +20%, +10%, -10%, and -20% under scenario 4, i.e., a drought frequency of once every 5 years.

We further doubled the sale rates of male animals (s_{ms}) from 18% to 36%, which led to only slight decreases of the population size in scenario 1while under scenario 4 (Fig. 4.11a and c, respectively), on average, the increased harvesting saved a non-significant number of the population per annum. Further, we assumed that milk availability to infants increased due to more forage available to females, which would reduce infant death rates (d_i); the increase in forage could be a direct result of an increased harvesting rate of male cattle. This assumed scenario saved a significant number (21%) of the entire population, particularly in scenario 4 (Fig. 4.11d).

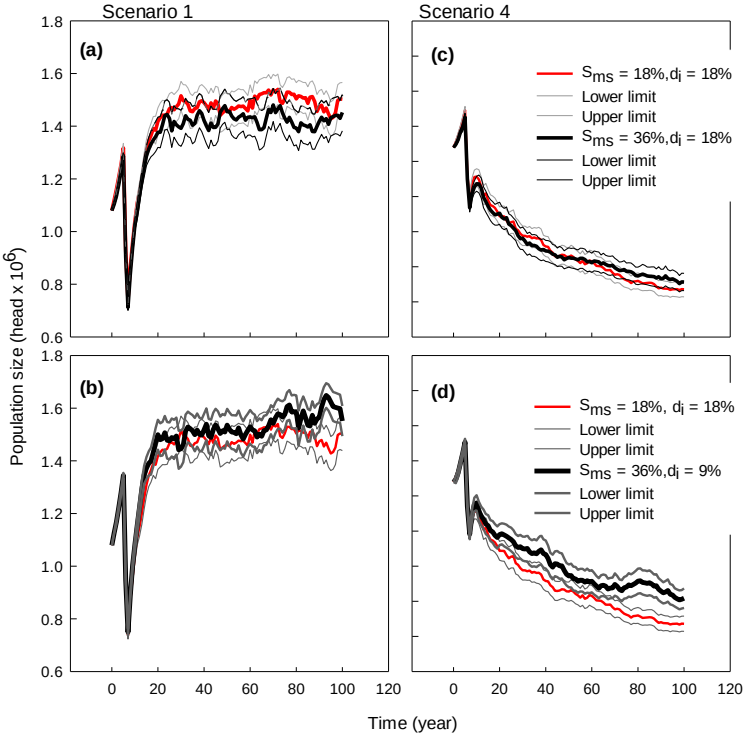

Figure 4.11 Cattle population trajectories with increased sale rates (s_{ms}) of senescent males (from 18% to 36%) and decreased death rate (d_i) of infants (from 18% to 9%) in scenarios 1 and 4 with a drought frequency of once in every 20 and 5 years, respectively. We ran the model 100 times over 100 years and averaged the population trajectory as shown.

4.4: Discussion

4.4.1: Boran cattle population trajectories

Population numbers drastically declined in our model when drought frequency increased, which confirms observations in Boran cattle populations during drought years (Angassa and Oba, 2007). The Boran cattle have been characterized to be well adapted to dry environments (Haile et al., 2011) and in our model, populations recovered quickly after each drought event. However, in scenario 4, i.e. when a drought occurred once every 5 years on average, which is very likely to happen in the near future in Borana, the Boran cattle resilience potential was reduced and the population declined by almost 70% in the long run. This is consistent with other studies who showed that herd crashes due to drought in Borana rangelands can reduce the population by up to 70% (Coppock et al., 2008; Forrest et al., 2014). Hence, drought events occurring every five years will have severe food security implications for pastoral communities, particularly in the face of climate change.

The pastoral communities have adapted to such environmental shocks in their management strategies through mobility, herding of different livestock species, and engaging in petty trades such as charcoal production or labor work in nearby towns (Yilma et al., 2009). Mobility is an important management strategy to provide rest to the pasture and prevent overgrazing (Breu et al., 2015). However, mobility is becoming more difficult in the Borana rangelands (Wario et al., 2016) and a herd size reduction through harvesting might be the best option in the long run to reduce localized grazing pressure and degradation. Our model showed that if we can keep the population below carrying capacity we can prevent it from extinction. This could be done, for instance, by yearly harvesting 36% more mature males than is currently done so that feed availability is increased for breeding females. Harvesting has been a successful strategy in Llama (Treydte et al., 2011) and zebra (Georgiadis et al., 2003) populations to keep populations stable. Alternatively, supplemental feeding can be provided through woody vegetation, pods, grass cuttings, etc (Abebe et al., 2012a; Angassa and Oba, 2008). However, it has also been shown that supplemental feeding can keep the populations artificially high (Müller et al., 2015), thereby even more depleting the last natural resources available. Therefore, supplemental feeding should be combined with the pre-planned animal sale to minimize the pressure on the environment in addition to a benefit from selling the animal before losing it to drought.

The current situation in Borana does not allow for a fast recovery of the cattle herd when drought frequently strikes because most of the key resource areas, which are potential fallback sites, are being turned into croplands (Angassa and Oba, 2008). However, cultivation alone cannot sustain the number of people that obtain their livelihood from pastoralism (FAO, 2009; Helland, 1998).

Generally, reducing herd sizes will significantly reduce the numbers of cows that have to be sold during drought (Birhanu et al., 2015) and decrease female death rates that is caused by feed shortages. Our results agree with Evans et al. (2010) who claim that external factors such as drought and markets strongly dictate the vital rates (births and death) in population dynamics. Further, the major impact of a drought is not direct but it aggravates the effects of other factors such as land use change, increasing human and livestock populations, raising the pressure on remaining forage resources (IPCC, 2001). Therefore, a drastic herd crash under increased drought scenarios highlights a need for appropriate rangeland management that contributes to adaptation and mitigation of climate change for a sustainable rangeland system (FAO, 2009) through resting and restoration of degraded areas. Appropriate management can be further augmented by an early drought warning system (Henricksen and Durkin, 1986) that encourages pastoralists to take an informed decision before the condition worsens in the face of environmental shocks.

4.4.2: Sensitivity analysis

The high influence of drought on external parameters (sale rates) in our model indicated that selling female animals is a more important factor dictating the future Boran cattle population size than the vital rates. This complements findings by Baptist (1992) who highlighted that the animal market strongly affects the future performance of a herd. As animal populations are rarely homogenous (Finkelstein and Cha, 2013) our model reflected the importance of harvesting males in an appropriate time before drought hits.

Models often take only the female population into account, excluding the male segment in their predictions (Cáceres and Cáceres-Saez, 2013). Our sex- and age-cohorts approach clearly showed how parameters strongly influence single cohorts within a population with varying effects. Berkeley Madonna has the advantage that the sensitivity of many parameters can be assessed at a time in both age- and sex-cohorts (Macey et al., 2009). Such information can aid in prioritizing the population group to be focused on in management so that the effect of drought can be accordingly buffered. Other population models have highlighted the importance of categorizing populations (Shabb et al., 2013) and using this as a tool to validate the projected population trajectory outcomes (Sargent, 2013; Treydte et al., 2011). Such sensitivity analyses represent an important tool for both calibration and validation techniques (Trucano et al., 2006) and show how essential monitoring data are (Kleijnen, 1995). Our sensitivity analysis revealed which sex- and age-specific cohort in a population most strongly affected the outcome of our model. This points out that data on mature female survival in particular needs to be understood for better prediction of future populations in the long run (Angassa and Oba, 2007). Often, there is a lack of such detailed purpose-driven data for modeling (Fox et al., 2012). We were fortunate enough to work

with a very detailed dataset, highlighting how essential it is to monitor population structure and dynamics, particularly for such a threatened cattle race as Boran (Zander and Drucker, 2008). Other population models have found that female survival is a parameter to which population model outcomes are most sensitive to (Treydte et al., 2011). We were surprised to find that calf mortality played a minor role in our sensitivity analysis, in contrast to findings by Coppock (1994). This might be attributed to the fact that calf mortality mitigation has already been a priority of cultural Boran cattle management e.g., through the provision of long-term exclosures, which set aside valuable grazing grounds for calves only in times of shortage (Dida, 2011).

In our modeling, we disregarded spatial variability, other grazing / browsing animals, and any social aspect, i.e., how herders feel about higher selling rates mainly due to the limited availability of demographic and long-term vegetation dynamics data. However, we still think that our model is a crucial step to understanding cattle dynamics within the rangeland system very well. Our face and internal validity techniques (Sargent, 2013) showed a good reproducibility of our model, as depicted by high R^2 values, and hence, provides some support that our model can be applied to the cattle dynamics under different drought scenarios in the face of climate change. Reproducibility is one of the most important attributes in evaluating a model (Taylor and Karlin, 1984). The need to have a parallel data set across which model predictions can be tested in the calibration process is also essential (Mayer and Butler, 1993). Our population simulations followed trends seen in an actual neighboring Boran cattle population.

As our model was stochastic, every run produced different output numbers (Oakley and Youngman, 2015; see also Appendix A Fig. 3-6). Such a model was found to be the most suitable model for semiarid areas (Sæther et al., 2000), such as Borana rangelands, which are characterized by both demographic and environmental stochasticity. The stochasticity helps to understand general mechanisms causing climate-induced population dynamics, which are poorly understood so far (Otto and Day, 2007; van de Pol et al., 2010) and management has learned to take variability into account (Coppock, 2016). Although, assessment of extinction risk is highly complex due to interacting stochastic processes operating on both density-independent and density-dependent components of population dynamics (Brook et al., 2008), cattle are the species with the highest number of breeds reported as extinct, thus losing its unique adaptive attributes (FAO, 2007). With this model, we were able to provide conservation recommendations to protect this important Boran cattle from extinction, which is mainly attributed to feed shortage caused by recurrent drought (Catley et al., 2014; Haile et al., 2011; Homann et al., 2003; Zander, 2011; Zander et al., 2009b). Globally, drought managements are largely based on ineffective crisis management (Wilhite et al., 2014, 2005). Likewise, in Borana rangeland drought management is highly vivid during a drought crisis. Our model can aid in devising a proactive drought management for age- and sex- structured

Boran cattle population in the face of more prevalent drought (He et al., 2014). Such strategies can enhance food security as they facilitate off take and prevent the build-up of herds and subsequent die-off of animals during drought, which has been a common phenomenon in eastern African rangelands.

4.5: Conclusions

The drought frequency has generally increased in Africa over the last 60 years (Spinoni et al., 2014) and predicting how livestock population trends vary under such increased drought frequency is a major challenge in ecology (Oppel et al., 2014). Currently, the Boran cattle are facing high herd crashes during drought events through increased mortality and an unplanned animal sale during drought. Our model outcome can help preventing these crashes by highlighting the importance of targeting animal cohorts in time before a drought crisis. We addressed this challenge in our model using random disturbance on population development under various drought scenarios. We incorporated drought as a randomly occurring disturbance in a dynamic cattle population model because cattle are highly vulnerable to drought (McCabe, 1987; Yilma et al., 2009). Our model output showed that an expected increasing drought frequency will strongly suppress the dynamics of Boran cattle population, leading to food insecurity in the long-run. Using differential equations, we tried to disentangle the mechanisms that cause drought-induced cattle population dynamics over a continuous time scale. Modeling stochastic demography and environment are of great importance in understanding cattle populations and determining herd sizes to fit the spatiotemporal variability of semiarid rangeland resources.

We recommend that there should be a market channel that encourages pastoralists to sell their animals before they lose body condition, and, hence, to fetch a better price. Cattle sale should be encouraged as it reduces grazing pressure on the rangelands; further, it should be pre-planned and should target males rather than females. In addition, drought early warning systems and market information must be strengthened in drought prone pastoral areas so that the advice of pre-planned selling can be realized. Further, rangelands should be managed to enhance resilience after drought through marrying scientific and indigenous knowledge.

Chapter 5: General Discussion

5.1: Grass biomass allocation under grazing and drought pressure

In our experiment, clipping highly reduced aboveground biomass of mature study grasses (*Cenchrus ciliaris* and *Chloris gayana*), which is consistent with similar observations in Kenya (Ngatia et al., 2015), South Africa (Mbatha and Ward, 2010) and China (Cui et al., 2005) as well as in Germany (Rose et al., 2013; Schmitt et al., 2013) and the Netherlands (Veen et al., 2014) for various grass species. This suggests that a resting period determines the quantity of the standing aboveground biomass (Pandey and Singh, 1992), and this seems to be irrespective of climatic conditions as it can be observed across the globe (Asner et al., 2004). Clipping/grazing further highly enhanced the belowground biomass (Chapter 2, Fig. 2.1), boosting the ability of grass to compete for water and nutrients (Engel et al., 1998). The enhanced belowground biomass due to herbivory was also observed in Spain (Garcia-Pausas et al., 2011), Argentina (Larreguy et al., 2014; Pucheta et al., 2004) and the Netherlands (Veen et al., 2014). This might be attributed to the reallocation of resources away from the site of damage and into storage organs after herbivory, which reduces the chance of resources being lost to herbivores (Gómez et al., 2010).

In contrast to mature grasses, the aboveground biomass in newly established study grasses was higher under moderate clipping compared to the control (Chapter 2, Figs. 2.2 & 2.4b), which concurs with studies from the Netherlands (Veen et al., 2014), USA (Frank et al., 2002) and in Mediterranean rangelands (Herrero-Jáuregui et al., 2016). The enhanced aboveground biomass might be attributed to greater photosynthetic capacity in younger leaves after clipping compared to the unclipped control (Nowak and Caldwell, 1984) and the overcompensation phenomenon (McNaughton, 1983). Clipping further stimulated the belowground biomass of newly established grasses, which concurs with many studies (Helland, 1998; Piñeiro et al., 2010; Pucheta et al., 2004; Smoliak et al., 1972; Veen et al., 2014). Grass roots play a significant role in grass survival (Hoogenboom et al., 1987), particularly in the face of increasing drought frequency due to climate change, which threatens the food security of the dryland regions of the world (Angassa and Oba, 2008; Keshavarz et al., 2017; Scoones, 1992). Hence, understanding differences in grass responses to herbivory can aid in devising appropriate management for rangelands of different ages. For instance, in Ethiopia (Tebeje et al., 2014) and Kenya (Koech et al., 2015) the selected study species have been recommended for reseeding in the frame of restoration at degraded rangeland sites. Hence, our results may increase knowledge and thus, rates of restoration of degraded areas (James et al., 2013; James and Carrick, 2016; Kakinuma et al., 2014). Restoration activities such as reseeding will enhance rangeland ecosystem resilience, which in turn improves the long-term food security of pastoral communities (Bedunah and Angerer, 2012).

Reduced irrigation amounts (long-term simulated drought) highly reduced both above- and belowground grass biomass of the two selected study species (Chapter 2, Fig. 2.3), which might be due to reduced non-structural carbohydrates (Chen et al., 2013), reduced CO_2 assimilation rate as a result of reduced leaf size and productivity (Farooq et al., 2009). Understanding grass responses to drought, a phenomenon that is expected to become more frequent, has paramount importance since drought is a major growth limiting factor in terrestrial ecosystems (Naudts et al., 2013) and further limits grass growth in the face of climate change (Fay et al., 2003, 2000). Therefore, grazing management should be adjusted based on known rainfall amounts in semiarid areas of Africa, particularly in terms of stocking rates (Kori et al., 2012). As the livelihood of the pastoralists in East Africa is mainly based on pastoralism that depends on an environment with patchy resources due to unpredictable climatic patterns that demand mobility (Flintan, 2012) and de-stocking in drought years as important rangeland management decision (Holechek et al., 1999) an adaptive management regime is crucial.

In our study, the combined effect of lower irrigation and more frequent clipping highly reduced the belowground biomass (Chapter 2, Fig. 2.4a), which might be attributable to reduced regrowth and leaf extension rate (Busso and Richards, 1993; Muthoni et al., 2014). Consequently, in newly established grasses, moderate and light clipping enhanced biomass allocation and, hence, should be considered as a post-reseeding rangeland management tool in restoration. Generally, areas with already established grasses should rest to replenish their aboveground grass biomass allocation while moderate grazing should be encouraged to stimulate its belowground biomass. Therefore, our results help in devising appropriate development strategies for better biomass yield in pastoral areas both for older rangelands and newly restored areas. A management that enhances belowground biomass should be encouraged since generally 92% of biomass is found belowground (Fan et al., 2009) and it plays an important role in the sustainability of rangelands (Acosta-Gallo et al., 2011).

5.2: Nutrient contents of rangeland grasses under grazing effects

Animal productivity in rangelands strongly depends on forage nutritive quality (Hussain and Durrani, 2009). The highly increased nutritive values due to clipping (chapter 2, Fig. 2.5) indicate that it is possible to boost the nutritive values of grasses through moderate grazing. Hence, grasses with enhanced nutrients can be used as a supplement to fortify rangeland grasses, for instance, to enrich protein ingestion during the dry season or drought period in areas where natural pasture is the main source of feed such as Borana rangelands (Tolera and Abebe, 2007). Low lignin and high protein contents are used as reliable criteria for forage quality (Sullivan, 1962). Herbaceous plants are deficient in protein when their nitrogen concentration is less than about 2.5% (Whitehead,

2000). In our experiment, both study grass species were poor in protein when mature as depicted in the nitrogen levels in unclipped grasses (1.73 % and 1.36% in *C. ciliaris* and *C. gayana*, respectively). However, clipping highly enhanced the crude protein content by up to 105% and 82 % in *Cenchrus ciliaris* and *Chloris gayana*, respectively. Further, clipping highly reduced the lignin content of the study grasses. Hence, this treatment contributed strongly to enhancing the forage quality of important rangeland grasses. In Borana rangelands, such improvement in quantity and quality of the perennial species can lead to conservation of the Boran cattle (*Bos indicus*) (Homann et al., 2004), which are threatened due to declining feed availability.

5.3: Grass carbon storage under herbivory and climate change

The response of carbon (C) followed the same pattern as that of grass biomass. Clipping highly reduced the aboveground C storage of the mature grass tufts (Chapter 3, Fig. 3.1), which agrees with results from Iran (Asgharnezhad et al. 2013). Conversely, grazing increased belowground C storage of mature grasses, which might be attributed to the reallocation of resources away from the site of herbivory as tolerance strategy (Babst et al., 2005; Gómez et al., 2010; Wise and Abrahamson, 2007). This implies that aboveground biomass management of rangelands has a critical impact on the belowground C storage and thus on long-term CO_2 emission mitigation (Gifford, 2010).

In newly established grasses, the light and moderate grazing stimulated the above- and belowground C storage of both study grass species (Chapter 3, Fig. 3.2) similar to studies by Veen et al., (2014). This stimulation might be attributable to greater photosynthetic capacity of younger grasses rather than older tissues (Nowak and Caldwell, 1984). In contrast, reduced irrigation highly reduced the above- and belowground C storage (Chapter 3, Fig. 3.4). our results suggest for *C. gayana* that under controlled clipping/grazing the predicted increase in rainfall in east Africa (Christensen et al., 2007) enhances the C storage of grasses. However, overgrazing might negatively override the positive effects of increased rainfall. Rangelands have been acknowledged to be a main sink for C as all soil organic C is primarily from plant origin (Kuzyakov and Domanski, 2000). Grasses have a potential to store C but are influenced by the available herbivore and rainfall and, hence, consecutive storage in soil will increase the overall C sink in the long-run (Wang et al., 2011).

Vast parts of global rangelands, potential C sinks, have already been degraded. Because of their vast area, a small change in soil C stocks across rangeland ecosystems would have a large impact on CO_2 accounts (Fynn et al., 2010). Overgrazing leads to rangeland degradation (Davies et al., 2010) as already observed in east Africa (Helland, 2001) and many parts of the world (Fernandez-Gimenez and Le Febre, 2006). Rangeland degradation further leads to a disappearance of

important native perennial grass species (Mganga et al., 2015). Restoring such degraded rangelands with perennial grasses can improve ecosystem goods and services (e.g. animal feed and C storage) as well as food security (Kimiti et al., 2017; Zimmermann et al., 2015). This can only be realized if there is a policy that encourages appropriate grazing management as manifested in our and other studies (Klein et al., 2007). A business as usual or a revert to the old rangeland management with mobile pastoralism seems difficult given the current situation (Helland, 2001). Hence, a new rangeland management approach, such as restoration through reseeding and post-reseeding management, should be the way forward under current and future scenarios for a sustainable use of rangeland resources (Costantini et al., 2016). As such, restored sites need a close technical follow up, for instance by appropriate pre- and post-reseeding management, i.e., assuring resting of older grasslands and timely reseeding until pastoralists adopt themselves to this new rangeland management approach so that the restored sites would not revert to pre-restoration state (Wairore et al., 2015).

5.4: Boran cattle population dynamics under limited rangeland resources

Responses of large herbivore populations to environmental constraints are strongly age- and sex-dependent (Gaillard et al., 2000). Hence, taking stochasticity into consideration across sex- and age-categories is a good approach for modeling population dynamics of large herbivores (Gaillard et al., 1998; Sæther, 1997). In our model, we included age-and sex cohort specific responses to carrying capacity variations. We further introduced drought as a random factor in our Boran cattle population model (Chapter 4), which caused the population size to continuously fluctuate. The environmental stochasticity and demographic stochasticity resembled actual trends in Boran cattle population trajectories under temporal variation. In semiarid environments droughts can cause livestock herd crashes (Ellis and Swift, 1988; Illius and O'Connor, 1999), which was reflected by our model, particularly under increased drought frequencies (Chapter 4, Fig. 4.8). To minimize the chance of a cattle population crash, the current drought management policy should be improved (Angassa and Oba, 2007), particularly in view of more common droughts predicted for the future (He et al., 2014). Further, in such a stochastic environment as a semiarid environment management should allow flexibility (mobility) and avoid reaching the carrying capacity through selling since a fixed carrying capacity is inappropriate (Campbell et al., 2006; Illius and O'Connor, 2000, 1999; Walker et al., 1987). Our model indicated that a pre-planned male cattle selling rather than females could minimize the herd crash during drought owing to removal of pressure from the rangeland that makes more feed available to females that results in more milk, which reduces the death rate of calves, a group most affected by drought (Coppock, 1994). Our models fitted the patterns of a real population over 12-years (Chapter 4, Fig. 4.6) and showed robustness, particularly under

increased drought frequencies (Chapter 4, Fig. 4.7). Consequently, we suggest that the drought management should focus on coupling the meteorological and early warning systems with market information so that the pastoral communities can pre-plan their animal sales and invest in other assets before the drought hits their cattle population. The results of this study can be used by policy makers to develop an appropriate strategy that helps the pastoral community to be proactive in coping with drought by reducing its impacts on cattle population.

5.5: Overall rangeland ecosystem resilience

Nowadays, at least 10-20% of the worldwide drylands and 70% of sub-Saharan rangelands are severely degraded (Millennium Ecosystem Assessment, 2005a). Hence, the capacity of rangelands to support the ever increasing human population is under challenge, particularly in the face of climate change. The human populations of rangelands are currently facing increasing instability, food insecurity, decreasing income, increasing poverty and a decline in adherence to social norms, mainly due to environmental degradation that has led to reduced resilience capacity of the system. Rangeland ecosystem resilience reduces when biodiversity declines (Millennium Ecosystem Assessment, 2005b) but shocks to the system (overgrazing and drought) can be buffered through restoring degraded sites by reseeding perennial grass species that have adapted to the dryland system. Further, improving post-restoration management through moderate grazing enhances grass resilience. As degraded ecosystem seem to recover slowly on a global scale (Moreno-Mateos et al., 2017) the resilience of degraded rangelands might also increase slightly. Restoration with perennial grasses enhances the sustainable utilization of rangeland by enhancing its productivity, which will be able to support important local cattle breeds that depend on rangeland feed resources. Management of rangeland is inextricably linked to different components of the rangeland ecosystem and can only be carried out practically in view of integrated biotic (herbivore, plant, and microorganism), abiotic (climate, soil nutrient) and anthropogenic (land management and herbivory) components.

Modeling such complex systems generally requires an understanding of relationships between the main grass stressors, herbivory and rainfall variability. The intention of a dynamic population modeling in our study was to give policy advice on strategies to improve herd management in the face of increasing drought. A comprehensive system of range use would include pastoralists adjusting their overall livestock numbers in relation to available biomass so that production and productivity of the rangeland and its livestock improve. Such strategies can enhance food security as they facilitate off take and prevent the build-up of herds and subsequent die-off of animals during drought, which has been a common phenomenon in eastern African rangelands (Angassa and Oba, 2007; Coppock, 1994; Scoones, 1992).

5.6: Study limitations and conclusion

We conducted our experiment on individual grass species under controlled irrigation and clipping with seeded grasses as well as mature tufts of the same grass species. Although such detailed experiments have been rare (Fidelis et al., 2013) they give a detailed understanding of how grasses of the same age respond to different treatments in the same environment. However, we are not sure whether the same result would be obtained in a natural environment, taking into account long-term vegetation dynamics under other potential factors such as pastoralist movement patterns or fire dynamics. Therefore, we recommend that similar experiments be repeated in the field on various grass species and over a longer time period. Such long-term experiments will also help to understand how much C is actually stored by the system in the long run as this process takes several years (Downs and Sala, 2009).

Further, in our modeling of the cattle population, we ignored other livestock and wild animal species in the area, mainly due to the lack of data. Hence, for the sake of simplicity, we assumed all grasses were consumed by cattle alone. However, the inclusion of other livestock species in future models could be helpful for a better understanding of the livestock population dynamics and its future trends in the face of climate change. In Borana zone, cattle are the dominant livestock species with about 41% the total livestock species in the zone (CSA, 2015). However, in some areas, browsing livestock species have become more popular, particularly in bush-encroached rangelands (Desta, 2013). Hence, including a higher variety of species will give advice on management options not only for the Boran cattle, the main sources of livelihoods in Ethiopian rangelands, but also other common livestock species such as camel, goat, sheep and donkey (Megersa et al., 2014).

In addition to livestock, the Borana rangelands harbor different species of wild animals. The common herbivorous wild animals in the Borana rangelands include Grevy's zebra (*Hippotigris grevy*), Burchell's zebra (*H. quagga*), gazelle (*Gazella spp*), warthog (*Phacochoerus aethiopicus*), lesser kudu (*Tragelaphus imberbis*), bushbuck (*T. scriptus*), Gunther's dik-dik (*Madoqua guenthen*), North African crested porcupine (*Hystrix cristata*), gerenuk (*Litocranius wallen*), oryx (*Oryx gazella*), Cape hare (*Lepus capensis*) and giraffe (*Giraffa camelopardalis*) (Coppock, 1994). In our modeling, we disregarded these wild animal populations as well as the negative relationship between rangeland components (such as bush encroachment and land use change) and carrying capacity due to the limited availability of demographic and long-term vegetation dynamics data. This could be a further step, including socio-economic and political issues such as access control/new movement barriers or the intention of the Ethiopian government to settle pastoralists

(Gebeye, 2016). However, we still think that our model reflects the current dynamics within the rangeland system very well, which was supported by our tests on robustness and validation.

Overall, this thesis provides an insight into plant-herbivore dynamics under climate change in a semi-arid rangeland of eastern Africa. Once highly productive, this rangeland has declined in quality and quantity (Solomon et al., 2007), calling out for urgent management interventions. Hence, our study contributes to knowledge on recommended herbivore pressure, re-seedable grass species, and overall cattle number management within a stochastic and highly fragile ecosystem.

Our study used a combination of varying techniques to understand rangeland dynamics in Borana (Fig. 5.1). Such combination of various data sets is important to understand a system more comprehensively (Scurlock et al., 1999).

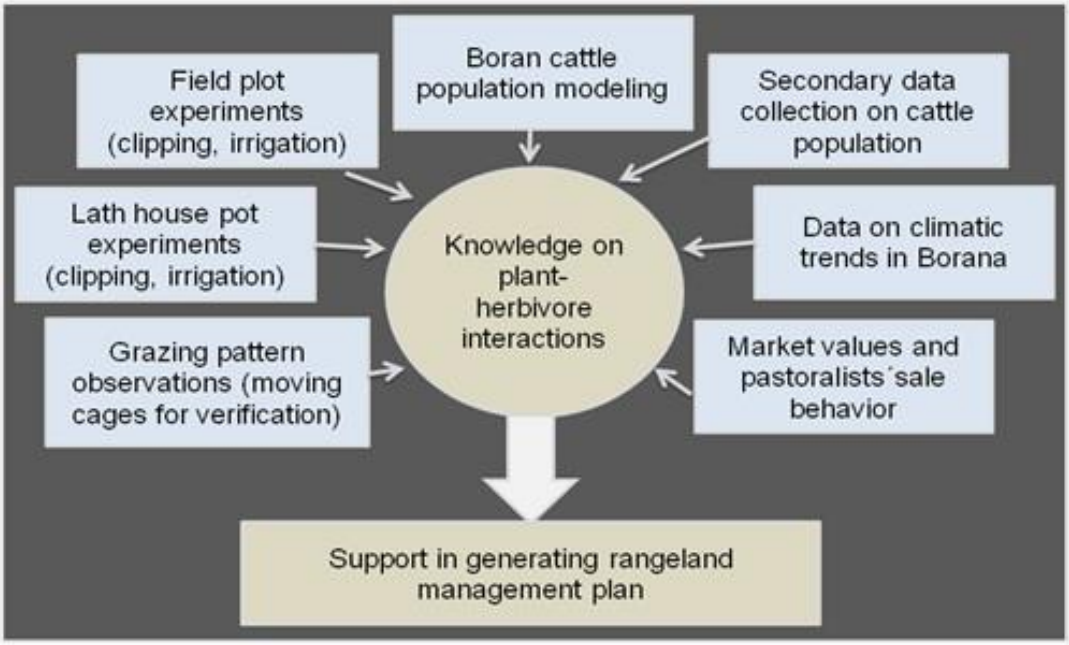

Figure 5.1 A combination of varying techniques used in our study to understand rangeland dynamics in Borana.

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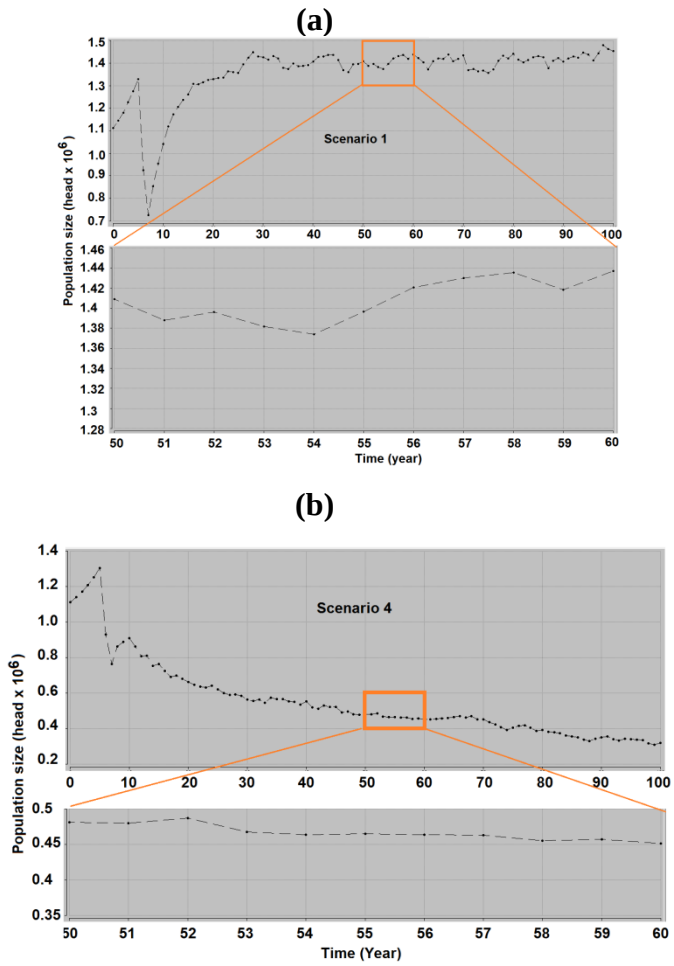
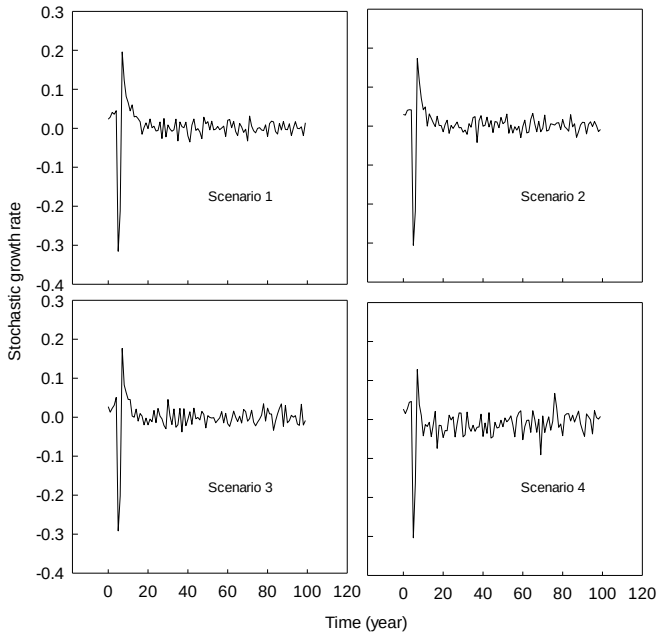
APPENDICES

Appendix A: Cattle population trajectories

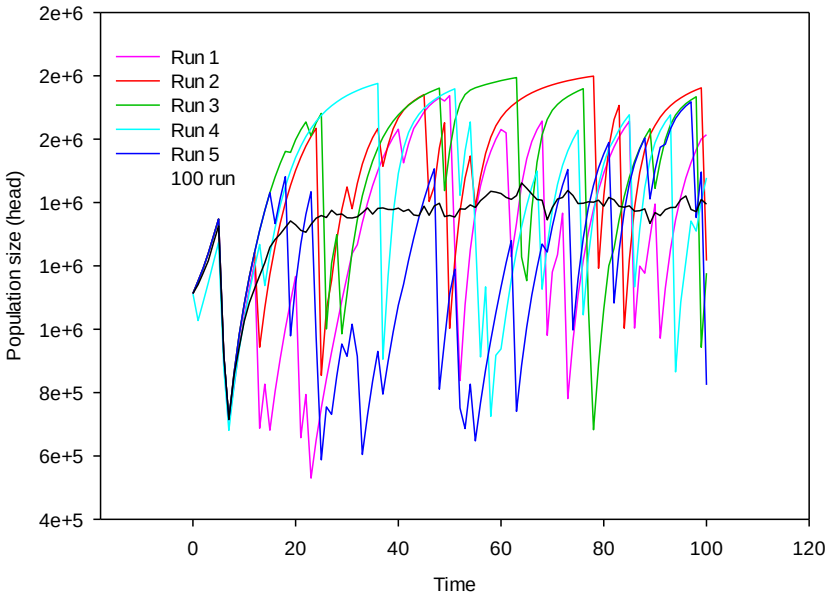


Appendix A Fig. 1. Population growth interval on an annual integration time step.

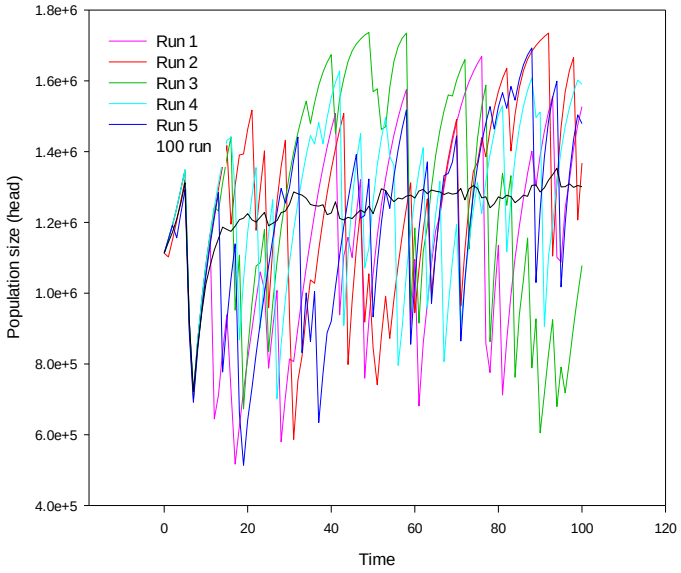


Appendix A Fig. 2 Stochastic growth rate of the Boran cattle population under the four drought scenarios (scenario 1 = once every 20 years, scenario 2 = once every 15 years, scenario 3 = once every 10 years, and

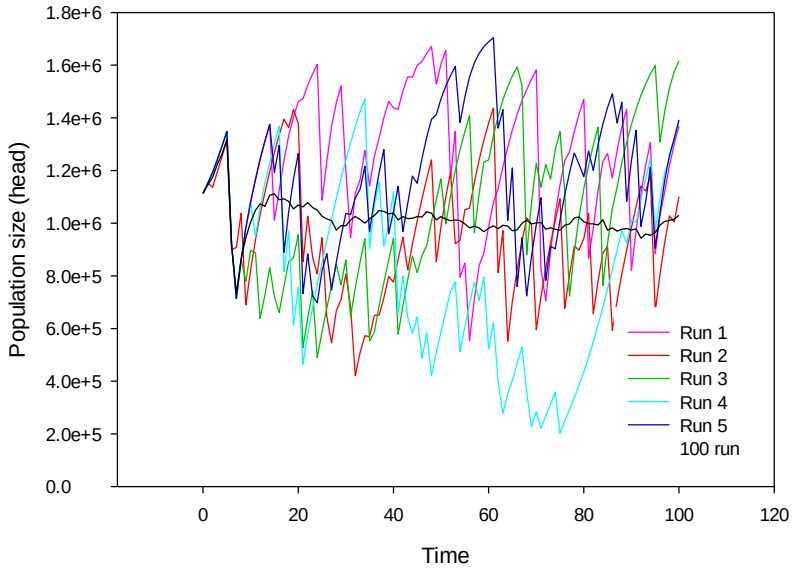
scenario 4 = once every 5 years). Population growth rate was calculated by the equation r = ((population at time step t+dt) - (population at time step t))/(population at time step t), for the average 100 time run model output under the four scenarios.



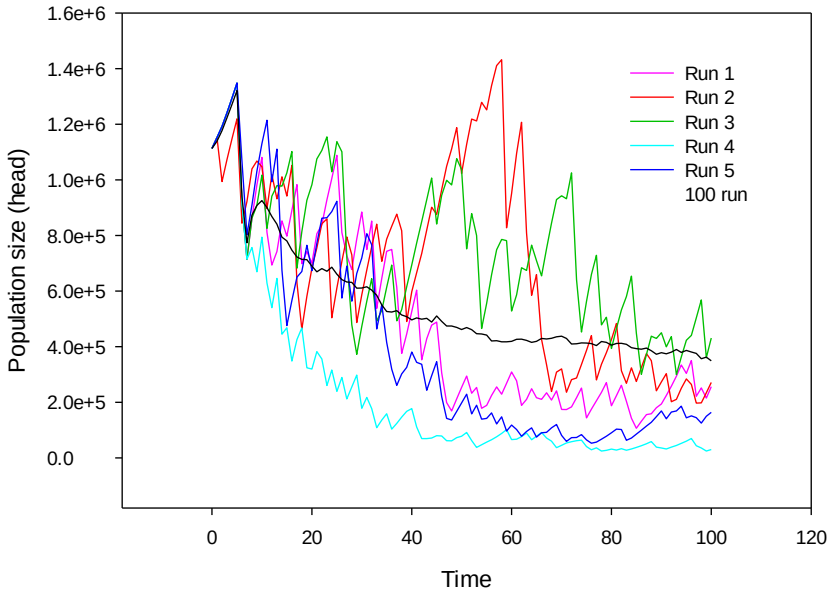
Appendix A Fig. 3. The five individual runs and the mean of 100 runs under stochastic logistic growth model of scenario 1.



Appendix A Fig. 4. The five individual runs and the mean of 100 runs under stochastic logistic growth model of scenario 2.

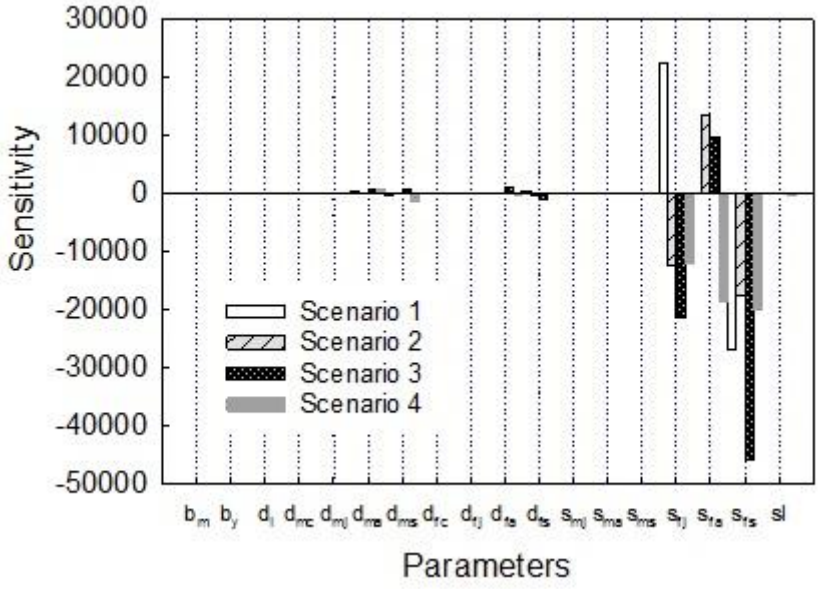


Appendix A Fig. 5. The five individual runs and the mean of 100 runs under stochastic logistic growth model of scenario 3.

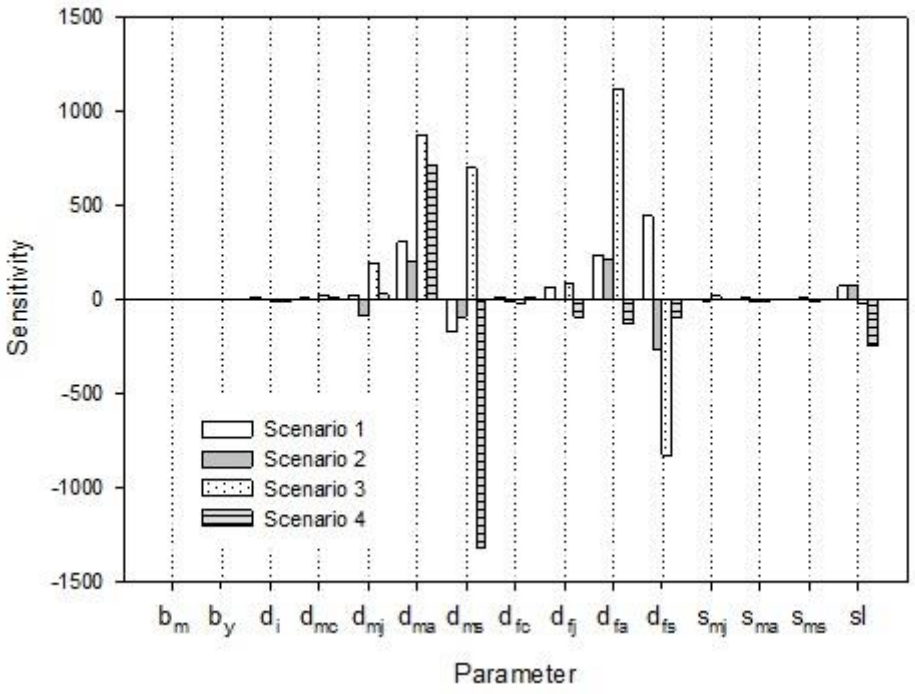


Appendix A Fig. 6. The five individual runs and the mean of 100 runs under stochastic logistic growth model of scenario 4.

Appendix B: Sensitivity analyses



Appendix B Fig. 1 Sensitivity of population size to model parameters. The model reacted most strongly to female sale rates. dmc = male calves death rate, dmj = juvenile male death rate, dma = adult male death rate, dms = senescent male death rate, dfc = female calves death rate, dfj = juvenile female death rate, dfa = adult female death rate, bm = birth rate from mature cows, K = potential carrying capacity, smj = juvenile male sale rate, sma = adult male sale rate, sms = senescent male sale rate, sfj = juvenile female sale rate, di = infant death rate, sfa = adult female sale rate, by = birth rate from young cows, sfs = senescent female sale rate, sl = slaughter rate.



Appendix B Fig. 2 Sensitivity of population size to model parameters after female sale rates were removed. The model reacted most strongly to senescent male death rates.